Does environmental selection for plant functional traits influence species' population trajectories?

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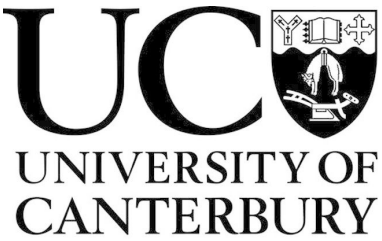

This thesis is

dedicated to my loved ones.

I could not have accomplished

this without you.

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Abstract

Humans appropriate ecosystem goods and services to maintain their quality of life. Consequently, anthropogenic activities have modified 40% of terrestrial ecosystems in a relatively short time. A major component of these modified systems are invasive species. Invasive species can drive a decline in native species richness and alter community structure, influence resource use and availability in their community, and in turn alter ecosystem functioning. Approaches analysing the similarity of traits between invasive and native species have become an increasingly common means to infer the processes underlying successful invasions and to predict future invaders. These approaches comprise part of a larger research context of understanding how species' traits link their response to environment, influence on ecosystem functioning, and interactions with other species.

In this thesis I used two overarching research questions to investigate whether environmental selection for plant functional traits influences species' population trajectories, which bears relevance for both native species decline and spread of invasives. These two questions were: a) How do environmental drivers of change influence species and trait composition (and can these influences be detected over the influence of spatial processes)? and b) how does the trade-off between competitive release (associated with novel traits) and environmental filters on community traits determine the success of species?

I addressed these questions by testing a number of hypotheses pertaining to each. To do this, I used data on plant communities over 30 years from grasslands across the South Island of NZ and sourced trait data to describe these communities from online databases. I used

a multivariate analysis framework to test for trait—environment relationships and describe how these relationships varied across multiple spatial scales. Additionally, I used measures of trait novelty and fit to environment, within a mixed modelling framework, to test how differences in these measures related to change in each species' abundance over time.

In doing so, I did not find support for my hypothesis that it is advantageous for species to have a novel (unique or original) set of traits, and that this advantage would be reflected in novel species increasing in abundance over time. Instead, I found that the environment shaped species traits, and that species with traits that deviated from those determined by environmental filters decreased in abundance. My findings suggest that searching for traits of 'invasiveness', or even comparing invader traits to those of the community, may have limited value in predicting the success of invaders unless these are considered within the context of environmental trait selection.

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Chapter 1

Introduction

1.1 Context

1.1.1 Global drivers of change

Humans appropriate ecosystem goods and services to maintain their quality of life (Pimm, 1997). Consequently, anthropogenic activities have modified 40% of terrestrial ecosystems in a relatively short time (Haberl et al. 2007). Land-use change, both current and historic, is ultimately driven by complex socio-economic conditions and an ever increasing population (MEA, 2005). However, changes in land uses and practices, such as deforestation and agricultural intensification, cause localised and widespread biodiversity loss and alteration of ecosystem function (Vitousek et al. 1997; Sala et al. 2000; Foley et al. 2005; Dobson et al. 2006). The outcome of such enterprise has led to the challenge of preventing global ecosystems decline (MEA, 2005).

Anthropogenic land-use change has had a largely negative effect on biodiversity. While there are examples to the contrary (Rudel et al. 2005), land-use changes typically homogenise the landscape, resulting in loss, fragmentation and modification of natural habitats. Habitat loss and modification lead to changes in species richness, relative abundance and composition (Fahrig, 2003; Newbold et al. 2016). While ecologists have long studied biodiversity, it is limited in its ability to link environmental change and ecosystem function through community dynamics (Stuart-Smith et al. 2013). Functional ecology provides a crossroads to overcome this limitation by focusing on species roles and functions within communities and ecosystems (Lavorel and Garnier, 2002; Westoby and Wright, 2006; Diaz et al. 2013). Accordingly, functional analyses are becoming increasingly popular as a way to describe ecological patterns and processes in greater detail, both within and across global biomes and throughout time (Lavorel et al. 1997; Diaz and Cabido, 1997; Guisan and Zimmermann, 2000; Diaz et al. 2004; Laliberté and Tylianakis, 2012). This is because functional traits act as a currency with which to account for changes in community dynamics and the mechanisms underpinning community assembly and ecosystem functioning (Poff, 1997), as they can determine how

species both respond to the environment ('response traits') and affect ecosystem function ('effect traits')(Suding et al. 2008).

Land-use changes may select for or against species on the basis of their traits (Larsen et al. 2005; Laliberté and Tylianakis, 2012; Rader et al. 2014). Furthermore, species composition and the diversity of species traits largely determine ecosystem function and services, such as provisioning of food and water (Foley et al. 2005; Hooper et al. 2005; Balvanera et al. 2006). As a result, species traits provide a pathway through which anthropogenically-induced degradation of ecosystems poses a significant risk to not only the world's ecosystems but also to the future of human well-being (Iii et al. 2000). Thus, understanding how species and trait composition are influenced by drivers of change is a central question in ecology.

1.1.2 Functional traits

Vegetation characteristics have long been known to strongly influence the internal dynamics of ecosystems through effects on resource supply (Vitousek et al. 1987), productivity and nutrient uptake (Grime, 1977; Chapin III, 1980; Field et al. 1992), litter quality and nutrient cycling (Hobbie, 1992; Breemen, 1993), and disturbance regimes (D'Antonio and Vitousek, 1992). Building from this work, the classification of plant functional types (e.g. woody, forb, grass, legume), based on correlations of traits between species, provided an effective means to generalise the principles on which plants respond to, and affect, their environment (D'Antonio and Vitousek, 1992; Keddy, 1992; Lavorel et al. 1997; Webb et al. 2010). Analyses based on functional types have proven their value in describing large scale (e.g. global or continental) vegetation responses to climate and effects on ecosystem function (Box, 1996; Diaz and Cabido, 1997; Bonan et al. 2002). At smaller local scales, analyses of functional types have improved understanding of responses to drivers such as nutrient gradients and disturbance regimes (Lavorel et al. 1997; Ni, 2003; McIntyre and Lavorel, 2001), and the relationship between biodiversity and ecosystem functioning (Tilman, 1997; Hooper et al. 2005). However, classification into categorical functional types inherently masks the

fine-scale biological variation between both similar and dissimilar organisms within a trophic level (Petchey and Gaston, 2006). The result of this is a loss of information pertaining to the mechanistic links between community functional composition and ecosystem processes (Lavorel and Garnier, 2002).

Functional trait-based approaches provide a means to overcome this limitation by focusing on species roles and functions within a community and the greater ecosystem (Poff, 1997; Westoby and Wright, 2006; Diaz et al. 2013). A functional trait is defined as a measurable property of an individual organism which strongly influences its performance or fitness (McGill et al. 2006; Webb et al. 2010), and which can be compared across species. Traits define species in terms of their ecological roles (i.e. effect traits), rather than evolutionary history, as well as how species interact with their environment and with other species (i.e. response traits; Diaz and Cabido, 2001). Recent works have identified that these two trait types are not mutually exclusive (i.e. a single trait can be both a response and effect trait). By using a combined response-effect trait framework (Lavorel and Garnier, 2002; Larsen et al. 2005), analyses of traits in plant communities have highlighted the importance of functional differences between species in response to soil resource availability (Laliberte et al. 2012), climate (Aubin et al. 2016), and disturbances such as grazing (Diaz et al. 2007), fire (Pausas et al. 2004a) and invasion (Eldridge et al. 2011), as well as an array of other global change drivers (De Deyn et al. 2008). Importantly, functional traits are better indicators and predictors of ecosystem processes than is species diversity (Loreau et al. 2001; Diaz and Cabido, 2001; Mayfield et al. 2010; Cadotte et al. 2011; Laliberté and Tylianakis, 2012; Naeem et al. 2012). Quantification of how abiotic and biotic drivers select for or against functional traits and determine community trait composition, within a context of global change, is thus required to anticipate how potential loss or modification of ecosystem function is likely to follow the erosion of biodiversity (Cardinale et al. 2012).

Functional diversity (i.e. the diversity of functional traits) can be used to describe the different aspects of variation in community functional composition and structure as a response

to disturbance and changes in environmental conditions (Diaz and Cabido, 2001; Folke et al. 2004; Mason et al. 2013b; Boersma et al. 2016). More generally, functional diversity represents the distribution and abundance of species traits in niche space (*sensu* Hutchinsonian niche, Holt, 2009; Petchey and Gaston, 2002, Villeger et al. 2008). Accordingly, the decomposition of functional diversity into various indices has become a popular method for the detailed examination of patterns of variation in niche space (Mason et al. 2005; Cornwell et al. 2006; Mason et al. 2007; Mason et al. 2008; Villeger et al. 2008). Moreover, such indices can be used to assess and quantify the functional dynamics underlying community assembly.

1.1.3 Functional traits and species invasions

In parallel with research on trait responses to the environment and influences on ecosystem functioning, a large body of work has attempted to use species traits to predict the success and impacts of invasion (see Gallien and Carboni, 2017 for a general review). This has proven difficult, as invasion is often context specific (Ricciardi, 2007; Sandel and Corbin, 2010; Pyšek et al. 2012), as well as time and scale-dependant (Pauchard et al. 2003; Loo et al. 2009; Buckley and Freckleton, 2010; Day and Buckley, 2011; Day and Buckley, 2013). Invasive species can drive a decline in native species richness and alter community structure (Alvarez and Cushman, 2002; Day and Buckley, 2013), influence resource use and availability in their community (Davis et al. 2000), and in turn alter ecosystem functioning (Pyšek et al. 2012). They often have characteristics such as fast growth rates and high fecundity (Grime, 1977), leading to a greater competitive ability and better exploitation of disturbance related opportunities (Grime et al. 1997; Burke and Grime, 1996; Keddy et al. 2002). These observations have led to a search for universal traits, processes and functional responses, which could unify invasion theory, and in turn enable the prediction of successful invaders (Baker, 1965; Rejmanek and Richardson, 1996; Williamson and Fitter, 1996; Daehler, 2003; Radford et al. 2010).

Approaches analysing the functional similarity between invasive and native species have become an increasingly common means to infer the processes underlying successful invasions and to predict future invaders (Webb et al. 2002; Leffler et al. 2014; Thuiller et al. 2010; Gallien and Carboni, 2017). Three main community assembly processes (or filters, Keddy, 1992) are thought to determine community trait composition when considering species invasion, or more generally changes in species abundances. These processes are (1) environmental, (2) biotic and (3) dispersal filtering (Theoharides and Dukes, 2007; Richardson and Pyšek, 2012).

Environmental 'filters' represent abiotic conditions that prevent the establishment or persistence of species in a particular location (Kraft et al. 2015). In the context of functional traits, these would be conditions which select for or against specific traits. For example, leaf size (e.g. specific leaf area) has been shown to have a strong negative association with temperature, because larger leaves experience a greater risk of freeze-fracturing of tissues or water loss through stomata. Thus, lower temperatures select for, smaller, more robust leaves, with thicker protective cuticles to reduce water loss (Rosbakh et al. 2015). Many examples exist of similar trait relationships which enable species to survive in an environment, such as increased bark thickness with fire frequency (Pausas et al. 2004b), reduced height and with nutrient availability (Falster et al. 2011) and leaf longevity with growth rate (Reich et al. 1999).

Second, biotic filters are essentially species or trait interactions which mediate the success of species (Luzuriaga et al. 2012; Crowther et al. 2014; Smith et al. 2015). For example, herbivore grazing acts as a biotic filter against palatable species, promoting the growth of unpalatable species (Begley-Miller et al. 2014). At the trait level, this reduces the average specific leaf area of plant communities (Zheng et al. 2015). Alternatively, plant-plant interactions may modulate the effect of environmental filters and assist to expand a species' realised niche (Holt, 2009; He and Bertness, 2014; Svenning et al. 2014; or promote niche differentiation, Zhang, 2003; Weber and Agrawal, 2014), such as when the canopy of

woody species facilitates or prevents herbaceous plant growth due to changes in soil water or light availability (Maestre et al. 2001; Villar-Salvador et al. 2008; Angelini et al. 2011; Angelini and Silliman, 2014).

Finally, dispersal filters act on the establishment of species (Funk et al. 2008). These filters may include processes underpinned by reproductive traits (e.g. isolation of a population patch, availability of seed in the regional pool; Alvarez and Cushman, 2002; Ozinga et al. 2005; Mayfield et al. 2006; Sonnier et al. 2010; Dehling et al. 2016), or vegetative traits such as the ability to spread in the local environment through clonality (Cornelissen et al. 2014; Dong et al. 2014). Confounding the understanding of each of these filters is the effect of the spatial scale at which each is observed or measured. Whereas at large spatial scales the signal of environmental filters is likely to dominate trait selection, at fine scales a complex mix of all three filters is likely to exert the greatest selection for traits (Gao et al. 2014; Trisos et al. 2014; Horn et al. 2015; Biswas et al. 2016; Asefa et al. 2017).

To understand how the relationship between traits and assembly filters facilitate species invasions, each of these components of community ecology needs to be addressed in turn. Then, considering how each of these act in concert will provide insight into the underlying dynamics of how selection for traits results in changes to species abundance. On one hand, species that occupy a novel region of trait space may suffer reduced competition (biotic filter) and thereby benefit via increased population growth. However, I hypothesise that species might be limited in their ability to escape competition by moving into new trait space, because environmental filters will select for trait similarity among species. Furthermore, I predict that it will be important to consider distinguish between vegetative and reproductive traits when testing this, because the latter is important for dispersal filters, and it has recently been shown that novel reproductive traits can come at a cost of losing mutualistic interactions (Coux et al. 2016), which could impose a new biotic filter to replace the competition. Moreover, our current understanding of how tradeoffs between the traits that allow species to pass through environmental filters, and those that allow them to reduce competition

(i.e. biotic filters) is limited. Understanding the premise of how these tradeoffs relate to changes in species abundance will prove beneficial to all those who are tasked in managing the restoration and conservation of invaded ecosystems (Hulvey and Aigner, 2014), as well as advancing invasion theory and preventing invasions in the face of increasing rates of global change.

1.2 Grasslands as a model system

Degraded ecosystems, including the degraded grasslands within this work was conducted, result from over-exploitation of resources or the alteration of disturbance regimes during land-use change. They occur when short-term (e.g. land-use change) or sustained perturbations (e.g. climate change) change the ecosystem's underlying abiotic and biotic conditions. Abiotic factors such as climate and soil composition and biotic factors such as competition and trophic interactions exert both top-down and bottom-up control of community assembly in the landscape (Hooper et al. 2000; Cramer et al. 2008). Disturbance factors such as fire, grazing and flooding modify both the abiotic and biotic conditions of systems in a dynamic, but consistent, manner within themselves (Menge and Sutherland, 1987). However, anthropogenic alteration of these factors facilitates alien species invasions (Didham et al. 2005) and induces range shifts and extinction of indigenous species, resulting in new biological communities (Duncan et al. 2001). In the case of significant perturbation, changes causing an ecological threshold to be surpassed may result in the system shifting into a state in which new abiotic and biotic conditions or interactions maintain the system in a degraded state (Suding et al. 2004; Lindenmayer and Luck, 2005). These new ecosystems may be vastly different than previous systems (Hobbs and Norton, 2004), in both species and trait composition (Pyšek et al. 2012), resulting in the loss or modification of ecosystem services. Furthermore, the alleviation of degrading factors may not be enough to reverse such change. This is particularly important for grasslands, where humans are dependant on them for their

ecosystem services yet they are undergoing rapid anthropogenically-induced change (Dixon et al. 2014).

1.2.1 Case study: New Zealand's high country grasslands in the South Island, and their change from pre-human to modern state

Recent research indicates that during the post-glacial period, conifer-angiosperm forest was dominant across 85-90% of New Zealand's below-timberline land area (Perry et al. 2014). The species composition of these forests formed a mosaic reflecting broad and fine-scale climatic, pedologic and edaphic conditions. This mosaic was most pronounced in the rain shadow of the South Island's alpine system (<1000 mm rainfall per annum). On lowland fertile soils, matai (*Prumnopitys taxifolia*), totara (*Podocarpus totara*) and kahikatea (*Dacrycarpus dacrydioides*) were dominant. Under drier climates (600-800 mm rainfall per annum), or where soils were less developed and where disturbance had occurred, these forests were likely interspersed with shrub communities of *Coprosma*, kanuka (*Kunzea ericoides*), manuka (*Leptospermum scoparium*), *Muehlenbeckia*, and other angiosperm small trees, shrubs and lianes. Compositionally distinct inland conifer-angiosperm dry forests formed in the semi-arid inter-montane basins and high country of mid-Canterbury (300-600m). The dominant podocarp species in these dry communities were bog pine (*Halocarpus bidwillii*), mountain toatoa (*Phyllocladus alpinus*) and thin-barked totara (*Podocarpus laetus*)(McGlone and Moar, 1998). The angiosperm component was spatially variable but well represented by small-leaved species such as kowhai (*Sophora microphylla*), kanuka, matipo (*Myrsine australis*), *Coprosma* and asterad shrubs. Together they formed a low open-canopy forest which intertwined with shrubby short tussock in the driest areas (<500 mm rainfall per annum) and alluvial flats. Pollen records show the most common non-woody constituents of these systems were silver tussock (*Poa cita*), hard (fescue) tussock (*Festuca novae-zelandiae*), and

the now rare native wheatgrass (*Elymus apricus*)(McGlone, 2001).

Evidence suggests that these woodland-shrubland areas were the only significant representatives of temperate grassland communities in New Zealand and were likely maintained by occasional natural fire (Walker et al. 2009; McGlone et al. 2014; Perry et al. 2014) However, there is on-going contention over the exact pre-human composition and extent of these grassland mosaics (i.e. Extensive: Walker et al. 2004; Vs. Limited: Mark et al. 2011). Notwithstanding this, it is well understood that the pre-human land cover was significantly altered by a wave of mega-disturbances including fire, pastoralism and land-use intensification. To understand how these disturbances have resulted in the largely degraded high-country landscape observed today, I will discuss each in turn.

1.2.1.1 Fire: The first wave of disturbance

Recent advances in our understanding of fire activity, both globally and in New Zealand, show that humans have rescaled the fire disturbance regime in both space and time, resulting in permanent, dramatic, widespread and rapid landscape transformation (McWethy et al. 2010; Bowman et al. 2011; Perry et al. 2014). Prior to human settlement, New Zealand existed as a largely forested archipelago (McGlone, 2001). Paleoecological records suggest that, during the early Holocene (c. 11,000 yr BP - c. 7000 yr BP), widespread fire would have been relatively infrequent in high country New Zealand (McGlone et al. 2014). Similar records indicate that during the mid-Holocene (c. 5000 yr B.P.) fire frequency increased in these areas, associated with drier summers driven by a strengthening of the El Niño Southern Oscillation (Ogden et al. 1998; Mcglone and Wilmshurst, 1999). Notwithstanding this, significant ignition events would still have been spatially isolated and temporally separated by centuries to millennia (Rogers et al. 2007; Perry et al. 2012b).

It is now well understood that successive human colonisation events and activities caused an increase in spatial and temporal frequency of severe fire in New Zealand. Most significantly, Polynesian arrival (from c. AD 1280+/-30 to c. AD 1600) marks the start of the

initial burning period (Perry et al. 2012a). Reconstruction of historic fire activity using charcoal records (McWethy et al. 2014) and other records indicate that during this period several asynchronous and severe fires occurred in the dry high country (McGlone and Wilmshurst, 1999; Perry et al. 2012a). Following this, during the Late Māori period (c. AD 1600–1850), palynological records suggest that widespread anthropogenic fire activity was maintained at a frequency of 50 to 100 years (McGlone, 2001). European settlement (c. AD 1850) was associated with a further increase in fire activity. These fires facilitated exploration, hunting, farming and other activities, which culminated in a reduction of dry forest cover from 84.1% to just 1.1% of its original extent (Rogers et al. 2005; Bowman and Haberle, 2010). The result of this was near complete eradication of once dominant dry-forest plant communities, extinctions of important avian browsers, seed dispersers and whole plant communities as well as a regression in the state of vegetation succession, and increased fragmentation and disruption of a wide range of ecosystem processes (Antonelli et al. 2011). Most significantly, these actions drove the expansion, and subsequently facilitated the maintenance, of a shrub and tall-tussock (*Chionochloa* sp.) grassland mosaic throughout the high country landscape (McGlone et al. 2014; Perry et al. 2014).

1.2.1.2 Pastoralism: The second wave of disturbance

European settlement in the mid-1800s marked the initiation of a second wave of extensive modification of the high country. Land clearance to facilitate pastoral exploitation and subsequent intensification, as well as the introduction of exotic plants and mammals, were the key drivers of the contemporary structure and function of high-country dry grassland ecosystems (Hobbs et al. 2006). On arrival, early European explorers of the high country were presented with approximately 3.3 million ha of fire induced shrub and tall-tussock grassland in various stages of succession after early Polynesian fires (See Figure 1. in Burrows, 1969). Initially, fire again proved to be a useful tool to clear shrublands to create and expand grasslands suitable for the introduction and grazing of sheep and cattle. Sheep grazing in the

high country reached peak numbers of approximately 10,000,000 stock units by 1900, often leading to over-grazing (O'Connor, 1982). Regular burning became important to maintain physiognomic grassland suitable for grazing, given a propensity to succeed to a woody state.

Concurrently, plants and mammals were deliberately and accidentally introduced during attempts to ease settlement and facilitate pastoral development. Notably, lagomorphs were introduced in 1830, with rabbits reaching plague (Connor and Vucetich, 1964) numbers throughout the high-country and decimating grassland productivity several times within the following century. Exotic pasture grasses (i.e. *Agrostis* spp., *Anthoxanthum odoratum*, *Dactylis glomerata*, *Festuca* spp.) and forbs (i.e. *Trifolium* spp.) were also deliberately introduced with the intention of enriching grasslands and increasing productivity (thus stock carrying capacity), followed later by over-sowing and aerial fertiliser application which were more common at lower elevations (below <900m). Unintentional introductions of invasive pest plants and animals have also occurred. Exotic plants such as the hawkweeds (*Pilosella* and *Hieracium* spp.) and conifers (*Pinus* spp., *Pseudotsuga menziesii*) have become invasive throughout high-country grasslands. Ultimately, systematically-poor land management in combination with species introductions has led to significant modification of the abiotic and biotic factors, as well as disturbance regimes, that previously maintained indigenous grassland ecosystems in their natural state. Furthermore, intensification, including cultivation and irrigation, is now resulting in an increased rate of change in these systems (Dymond et al. 2017).

1.2.1.3 Current states of New Zealand's high country

The legacy of the above anthropogenic activities imparts the contemporary distribution, structure and function of grasslands in New Zealand. The high country landscape is now largely dominated by anthropogenically-induced depleted short-tussock grasslands, except where some tall tussock communities persist at higher elevations (Day and Buckley, 2013). These grasslands are characterised by a reduction in vegetation stature and density, a shift in

tussock species composition, the loss of inter-tussock communities, and a significant exotic species component (Duncan et al. 2001; Day and Buckley, 2013). The modification of abiotic factors such as water and light availability, and the influence of biotic factors such as introduced herbivorous mammals (instead of now extinct avian browsers and seed dispersers) and plants, as well as dynamic interacting feedbacks between these factors, have led to the transgression of ecological thresholds which act to constrain vegetation succession to a novel trajectory and ecological state (Standish et al. 2008). These positive feedbacks inhibit natural succession to a native dominated woody-grassland community (Standish et al. 2008). Importantly, these factors and their feedbacks have framed the depletion and loss of the indigenous component of tussock grasslands, and facilitated their invasion by exotic plant species (Day and Buckley, 2011). Similarly, these pressures have exacerbated shifts in the composition and diversity of plant functional traits, the long-term effect of which is fundamental changes to ecosystem function (Laliberté and Tylianakis, 2012).

Consequently, significant research effort is required to investigate how these environmental pressures select for certain functional traits, and in turn how the composition and diversity of traits influence species abundances. Such knowledge will enable new insight into the novel dynamics of grassland vegetation, both in New Zealand and globally, as well as assist us in the conservation of indigenous species, the management of exotic species, and as the stewards of ecosystem states.

1.2.1.4 Conservation of high-country dry-grassland ecosystems

In New Zealand, 15.4% of the original (1840) extent of grasslands now consists of formally protected areas (Figure 2 in Mark et al. 2009). However, there are shortcomings in the conservation of short-tussock grasslands. Firstly, only 5% of the national total of protected grassland area can be attributed to the protection of these short-tussock ecosystems (Mark et al. 2009), which represents potential habitat for rare, threatened species. Furthermore, pressure from surrounding land-use intensification (e.g. pivot irrigation) and exotic herba-

ceous species and woody encroachment present on-going ecological challenges, increasing the vulnerability of these areas to further degradation (Weeks et al. 2013a; Weeks et al. 2013b). Second, contention over the pre-human extent and distribution of woody vegetation in the high-country compound these conservation challenges by generating dichotomies in the management of disturbance (e.g. the role of grazing; Rogers et al. 2005) and the long-term conservation goals for tussock grassland (Walker et al. 2004; Mark et al. 2013). Notwithstanding these issues, research efforts are beginning to focus on the long-term restoration of native woody communities in depleted short-tussock grasslands. In light of this, it is of great importance to assess how environmental selection of plant traits and competition may influence the persistence of species, as indicated by changes in their abundances over time. This knowledge will contribute toward understanding the constraints on trait-based community assembly processes in grasslands, and thus advance our knowledge of how to better manage these increasingly novel ecosystems.

1.3 Summary, aims and hypotheses

In summary, the literature reviewed above highlights the importance of understanding the tripartite relationship between species, traits, and the environment in the context of widespread environmental degradation. Additionally, I have illustrated the important role that functional traits play in the maintenance of biodiversity in ecosystems, using concepts rooted in community ecology and invasion theory. In discussing the natural history and current status of New Zealand's South Island high country grasslands, I have given background to the globally relevant grassland ecosystem, which I am using as a study system. Using this system, I will investigate how the abiotic and biotic environment and competition select for plant traits, and how these processes may influence future trajectories of species abundances. Furthermore, it is already well known that environmental conditions can vary across spatial gradients, which can make it difficult to distinguish between environmental drivers of com-

munities and spatial processes that lead to autocorrelation (Dray et al. 2012). Therefore in examining the environmental drivers of community species and trait composition, I place heavy emphasis on partitioning the influence of environmental vs. spatial processes.

I investigate this topic by addressing two broad research questions.

1. How do environmental drivers of change influence species and trait composition, and can these influences be detected over the influence of spatial processes? and

2. How does the trade-off between competitive release (associated with novel traits) and environmental filters on community traits determine the success of species?

To answer these questions, I will be using community composition data, measured over 30 years in locations throughout my study system, in combination with species trait data compiled from on-line databases, publications and herbarium specimens. I discuss these data in Chapter 2. Because environmental, biotic and dispersal filters can differentially select for vegetative and reproductive traits I separated these two trait types. Following this, I present the methods and results for each of my research questions separately. Chapter 3 describes the multivariate methods which were used to disentangle the spatial and environmental drivers of species and trait community composition. The results of these analyses are presented in Chapter 4. Chapter 5 outlines the functional diversity indices and mixed-effect modelling framework used to address my second question. There, I hypothesise that it is advantageous for species to have a unique set of traits, and that this advantage will be reflected in unique species increasing in abundance over time. However, it is unclear whether selection of traits by the environment will overwhelm these effects. The results of these analyses are presented in Chapter 6. Finally, in Chapter 7, I bring these two topics together in a discussion.

Chapter 2

Study Data

2.1 Data

2.1.1 Species Data

The species abundance data used to carry out analyses were drawn from the National Vegetation Survey Databank (NVS) (see Wiser et al. 2001) [1].The data consists of plant taxa measured along 100 m transects at 125 permanently-marked sites located in tussock grasslands of the lower South Island, New Zealand (Figure 2.1). Observations of environmental conditions accompany each transect measurement, and includes data on climatic conditions, soil properties, land-use types, and evidence of disturbance (discussed below). The methods for vegetation sampling, as well as characterisation of the site environments, follow a modified Wraight permanent plot protocol and are extensively detailed in Duncan et al. (2001). Each transect was established between 1982 and 1986 and all transects were remeasured twice, first during 1993 and 1998, then again between 2005 and 2007 (Buckley and Freckleton, 2010; Day and Buckley, 2011; Day and Buckley, 2013) providing a record of vegetation change at each site over approximately 30 years at varying intervals. The purpose of these transects is to assist with the monitoring of vegetation and various land management decisions, and each contributes to the Lands and Survey permanent grassland transect collection (H. Buckley, pers. comm.).

Duncan et al. 2001 made the following observation, "Although the original 144 transects are not a random sample of tussock grasslands throughout the study area, their history of land-use is representative of high-country grasslands throughout the South Island, and range-lands world wide, with an early period of 'exploitative' pastoralism followed by absent or relatively low levels of anthropogenic disturbances such as grazing and burning during the current 'restoration era' ". The 125 transects utilised in this study are a subset of the 144 used by Duncan et al. 2001 to identify the effect of various land-use and management regimes

[1] I Zane W. Lazare acknowledge the use of data drawn from the National Vegetation Survey Databank (NVS) on 21/12/2015. These data were provided with the permission of Hannah Buckley, School of Science, Auckland University of Technology, NZ.

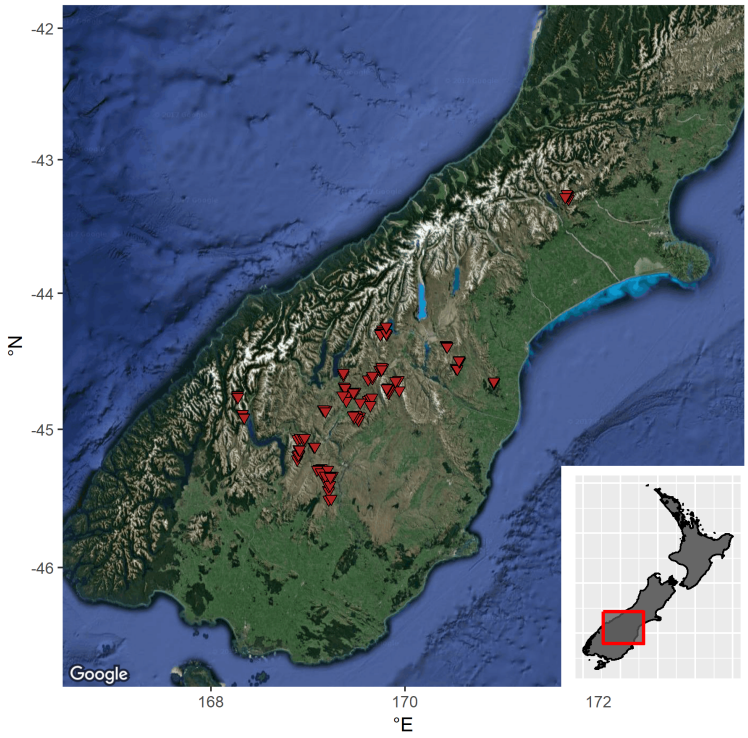


Figure 2.1: Map showing the location of transects used in this study

on plant species richness in tussock grasslands. Twenty-four transects of the Duncan et al. (2001), Buckley and Freckleton, (2010), Day and Buckley, (2011), and Day and Buckley, (2013) were excluded from this study's dataset as they did not have measurements for all time periods. The remaining 125 transects are spatially clustered occurring on 29 properties, with between 1 and 10 transects on each individual property.

The vegetation cover data used for analyses contained 358 taxa in total across the entire study period. Of these, 294 were native species (82%) and 64 were exotic (18%).

2.1.2 Trait Data

I collected trait data for each species in the data set, and described twenty four traits to represent major aspects of variation in growth, survival and reproduction strategies of each species. I separately described both vegetative and reproductive traits following the standardised protocols of Perez-Harguindeguy et al. 2013 and Cornelissen et al. 2003. Each

trait was chosen based on its ability to be described *ex situ* (i.e. using publicly available resources), and reflects a maximum population value. Each trait included has been demonstrated to relate to a wide range of natural and human driven processes, including changes in biodiversity, dynamics in species invasion, change in bio-geochemical processes, and plant-atmosphere interactions (Vandewalle et al. 2010).

I obtained trait descriptions from across several digital and physical resources. These resources included the online database of Landscare Research (ecotraits.landcareresearch.co.nz/), the New Zealand Plant Conservation Network (nzpcn.org.nz/) and several book resources (Allan et al. 1961; Stuppy, 2003; James et al. 2012). Some trait measurements were obtained from voucher specimens at the University of Canterbury Herbarium, and when sufficient samples were available I took an average of measurements from at least five specimens. Descriptions of each trait are listed in Table A.1.

2.1.3 Study Site Data

The sampling range of sites geographically encompasses a wide array of environments associated with tussock grasslands. Transect location varies in elevation from 371 to 1882 m above sea level, covers a range of rock and soil types, and includes vegetation types ranging from high altitude native tall tussock grassland to highly modified, lower-altitude, exotic dominated communities and short tussock grassland (Duncan et al. 2001).

In order to understand the influence of the environment on species and traits, I used a set of environmental variables collected for each transect at the final sampling occasion. These environmental variables included climatic variables (e.g. mean temperatures and rainfall) and details of the growing substrate (e.g. chemical properties and parent-rock types). In addition to these variables, transects were subject to two land-use types, government conservation or Crown-leased pastoral. Of the 125 transects at the time of measurement, 16 occurred within boundaries of conservation land and 109 were located within pastoral land. These land-use variables were also included in analyses. Environmental explanatory

variables and their abbreviations descriptions are presented in Table 2.1.

Table 2.1: Descriptions of environmental variables collected for each transect at in this study and used to test trait-environment relationships at the final sampling occasion. See Buckley and Freckleton, 2010 for further details.

Abreviation	Variable	Type	Value and/or Units
Soil properties			
CEC	Cation exchange capacity	Continuous	Integer
Saturation	Base saturation	Continuous	%Water weight
Ca	Calcium	Continuous	$me/100g$
Mg	Magnesium	Continuous	$me/100g$
P	Potassium	Continuous	$me/100g$
Na	Sodium	Continuous	$me/100g$
P	Phosphorus	Continuous	$\mu\ g/ml$
S	Sulphur	Continuous	Parts per million
BlkDens	Bulk density	Continuous	Grams of dry soil per volume of soil
Parent material			
Soil	Soil type	Catagorical	Brown, Gley
Rock	type	Catagorical	Greywacke, Schist
Climate			
Precip.	Precipitation	Continuous	Normalised 30 year average of mean monthly precipitation (mm)
Temp.	Temperature	Continuous	30 year average of mean monthly temperature (degrees celcius)
Land use			
	Tenure type	Categorical	Pastoral, Conservation
	Grazing	Catagorical	Grazed, Not grazed, Grazing removed
	Previously burnt	Catagorical	Burnt, Not burn
Other			
Solar	Solar exposure	Continuous	Watts per/m^2
Slope	Site slope	Continuous	Degrees
Aspect	Site aspect	Continuous	Degrees

Chapter 3

Methods: How do environmental drivers of change influence community species and trait composition?

3.0.1 Summary

The first aim of this thesis was to determine how the environment shapes community composition in terms of species and traits. Because the data came from sites across a large spatial extent, yet with some clustering of sites into properties, it was necessary to identify and account for any spatial structuring in the community data. To achieve this, I used two methodological frameworks, the combined fourth-corner RLQ analysis (Dray et al. 2014) and Moran's Eigenvector Maps (Dray et al. 2006). These frameworks both heavily employ ordination procedures, and in combination enable the spatially-explicit testing and characterisation of direct, indirect, and interacting drivers of change on community composition. The first framework, Moran's Eigenvector Maps [MEMs] (Dray et al. 2006), consists of characterising and decomposing variation in both response (e.g. species and trait composition) and predictor (e.g. environmental) variables, which is attributable to spatial structuring. The end goal of this method is to produce a set of models which characterise spatial structuring in both response and predictor variables, which then may then be used to test hypotheses at discrete spatial scales. The second framework, combines the fourth-corner (Legendre et al. 1997) and RLQ (Dolédec et al. 1996) methods for assessing trait responses to environmental gradients (Dray et al. 2014). While both methods are based on analysis of the fourth-corner matrix, RLQ is a multivariate technique which summarises species-trait-environment relationships, whereas the fourth-corner method mainly tests for individual trait-environment relationships. Together these methods represent the most integrated means to analyse trait-environment relationships (Kleyer et al. 2012). Each method is discussed in detail below in the order required to carry out the analyses.

3.1 Methods to detect spatial patterns in species and trait composition

3.1.1 Moran's Eigenvector Maps (MEMs) and spatial model selection

3.1.1.1 Computation of Spatial Weighting Matrix

Moran's Eigenvector Maps (MEMs) (previously known as Principal coordinates of neighbour matrices; Borcard and Legendre, (2002), Borcard et al. (2004), and Dray et al. (2006)) provide an elegant means to construct sets of linearly independent spatial variables which can be used to account for spatial autocorrelation in modelling exercises and characterise types of spatial autocorrelation in datasets. In addition to this, groups of eigenvectors showing similar patterns of variation may be exploited to define subsets of models which reflect processes occurring at distinct spatial scales (Peres-Neto and Legendre, 2010; Brind'Amour et al. 2005).

The procedure for creating Moran's Eigenvector Maps consists of two components: a) creating a list of links among study sites using a connectivity matrix and b) constructing a matrix of weights to be applied to these links, which represent the ease of exchange between the points connected by the links (Dray et al. 2006). The Hadamard product of these two matrices results in a final spatial weighting matrix which is then used for subsequent analyses.

The choice of spatial weighting matrix is the most critical step in spatial analyses as it defines the interaction between sites (Mauricio Bini et al. 2009). Theory-driven specification can be utilised where it is based on sound biological knowledge, for example when an investigator has an understanding of barriers to dispersal (Fall et al. 2007; Dale and Fortin, 2010). However, in general it is advised to use a data-driven approach (Legendre and Legendre, 2012), which makes no a priori assumptions about the nature or extent of linkages among

sites. Therefore, for each species and trait dataset, I defined 10 connection networks based on community similarity over a distance sequence between a minimum and maximum. The minimum distance was selected as the minimum distance which kept all sites connected in the network (threshold distance, see Borcard and Legendre, 2002) and the maximum was the longest distances between two sites. Sites that fell within these two parameters of each other were considered connected. For each network, an iterating range of distance-decay weighting functions were applied to the links. Each weighting function was based on Euclidean distances among the sites: $f_2 = 1 - (d/d_{max})^a$, where d is a link's distance value, d_{max} is the maximum value in the distance matrix, and a iterates from $2 - 9$, producing a total of 90 candidate spatial weighting matrices. I then calculated the eigenvectors and ordered them according to their explanatory power for the dataset of each of the model candidates using the *test.W* function (R package *adespatial*, Dray et al. 2016). The spatial-weighting matrix with the lowest corrected Akaike information criterion (AIC_c) was retained as the model of best fit for the global spatial structuring. This process was repeated twice thereafter, first to obtain only eigenvectors with positive Moran's I values and second to obtain eigenvectors with negative Moran's I values, thus enabling the separate analysis of positive and negative spatial autocorrelation respectively.

3.1.2 Visualisation of spatial patterns in species and trait composition

Patterns of spatial diversity in species and traits for the final sampling occasion were first visualised by plotting multivariate community and trait data against their geographic coordinates. The community species matrix was Hellinger transformed to standardise observational data and downweight the importance of dominant species because of the high number of species with few occurances (Legendre and Gallagher, 2001). Community-weighted means represented the compositional data for both vegetative and repoductive traits at each site (Peres-Neto et al. 2017). The sites scores of a principle component analysis (PCA) were

then plotted on their geographic coordinates. A redundancy analysis (RDA) procedure was then carried out on the resulting PCA to quantify the variation associated with environmental variables, while partial residual analysis (PRA) was used to remove the effects of measured environmental variation and focus on only the residual variation which could be attributed to my spatial variables. Plots showing the correlation of the first two axes of RDA to environmental variables were used to highlight strong environmental gradients. The spatial component of each dataset was examined using the MEMs previously described (Section 3.1.1.1). For each PCA, RDA and PRA, scalograms were computed by projecting the sites scores of the first two axes of the different analyses onto the spatial basis formed by the dataset's MEMs. R^2 values for each eigenvector were then tested for significance using a permutation procedure (with 999 repetitions) (Dray et al. 2012). Carrying out each step of these analyses provided an insight to the level of spatial diversity of species and traits, how these components of diversity are structured by the environment, and to what extent spatial autocorrelation exists in the data.

3.1.3 Local and regional structures: Eigenvector decomposition

3.1.3.1 Variation partitioning

Variation partitioning is a statistical method which attempts to partition the explanatory power of multiple explanatory matrices in relation to a single response matrix. The method is widely used in ecology to separate and compare the components of variation in species abundance data associated with environmental, spatial and temporal variables, as well as that which cannot be attributed to any measured variables (Borcard et al. 1992; Legendre et al. 2005; Gravel et al. 2008; Bienhold et al. 2012; Gobet et al. 2012). In this study I partitioned the variation associated with environmental variables and MEMs (the latter representing spatial processes) to examine the magnitude of their effect on both species and trait community composition data. In particular, I compared the fractions of variation contributed by MEMs associated with positive and negative spatial autocorrelation. I then

used this information to define the scope of subsequent spatial analyses and focus on spatial structures associated with broad (regional) and fine-scale (landscape) negative spatial autocorrelation (discussed later in Section 3.1.3.2).

To carry out the analysis, I used the modified technique of Peres-Neto and Legendre, (2010). This method differs from the original of Borcard et al. (1992) in that an individual species (or trait) based forward selection of explanatory variables is used to reduce the number of model parameters (Blanchet et al. 2008), thus increasing the power of the test (by increasing available degrees of freedom) and reducing the risk of inflated type I error rates associated with parameter selection to an acceptable level (Wilkinson and Dallal, 1981; Dutilleul et al. 1993; Legendre et al. 2002; Mundry and Nunn, 2009). The forward selection procedure accomplishes this by enforcing a double-stopping criterion when introducing new parameters into the model. I implemented the modified analysis as follows: 1) carry out an RDA of each species and trait data set with respect to each explanatory matrix (i.e. environment variables, MEMs [$+ve$ and/or $-ve$] and site location coordinates [XY]) , 2) test each RDA for significance using ANOVA (with 1000 repetitions), 3) if significant, carry out forward selection of the explanatory variables using a double-stopping criterion before proceeding with including them in the variation partitioning model. The two stopping criteria were a) the usual alpha significance level ($p < 0.05$) and b) the adjusted coefficient of multiple determination (R^2_a) calculated using all the explanatory variables (i.e. adjusted R^2 of the initial RDA). When a variable is introduced that brings either of the criteria over the fixed threshold, that variable is rejected and the procedure is stopped. In the case of MEMs, I applied forward selection *a posteriori* to the original AIC-based spatial-model selection procedure prior to being included in the variation partitioning. Each fraction of variation was then tested for significance by ANOVA (again with 1000 repetitions). The resulting subset of environmental and spatial predictors was then used for further analyses. The the functions 'rda', 'varpart', 'RSquareAdjust' and 'forward.sel' in the R packages Vegan (Oksanen et al. 2017) and ADESpatial (Dray et al. 2016) were used to perform this analysis.

3.1.3.2 Spatial sub-model selection

As previously mentioned in Section 3.1.1.1 MEMs may be used to construct sub-models reflecting processes occurring at discrete spatial scales. A full set of MEMs consists of the number of sites -1 eigenvectors and they have a straightforward interpretation as spatial correlation templates. Each eigenvector provides a decomposition of the spatial relationships among sites and can be interpreted in terms of separate spatial scales (Dray et al. 2006). Definition of spatial-predictor sub models is enabled by grouping eigenvectors accordingly depending on the similarity of their semi-variance across the study area. When the MEMs are computed from a regular sampling design (e.g. an equi-spaced transect or grid) the resulting variables represent a series of sinusoids of decreasing periods (see Legendre and Legendre, 2012), and spatial sub-models (reflecting arbitrary spatial scales) may be classified using principles applied to Fourier transforms (Renshaw and Ford, 1984; Munoz et al. 2007). In the case of irregular sampling designs (as in this study) eigenvectors lose the regularity of their shapes making the assessment of their scale difficult (Borcard et al. 2004).

Only MEMs showing negative eigenvalues (negative Moran's I) remained with multiple variables following the computation and forward selection for each data set (only one variable with positive Moran's I remained for each case). Therefore, I used only MEM variables characterising negative spatial autocorrelation to create sub models reflecting spatial scales. To define the sub models and their respective spatial scales, I projected the values of each eigenvector on to a map of the study sites and produced an accompanying variogram (presented in the results). I grouped each of the eigenvectors by visual inspection according to whether they showed regional ($> 120km$) or landscape ($< 120km$) scale spatial accumulation of semi-variance. These groupings thereon in were used to represent spatial processes occurring at regional (broad) and landscape (fine) spatial scales associated with greater spatial diversity in community composition than at random.

3.2 Environmental selection of traits

3.2.1 Multivariate species-environment-trait relationships: RLQ method

The above sections explored spatial patterns in community and trait composition, and provided a basis for understanding the scales at which non-random differences in community traits among samples were most apparent. Subsequently, I explored the extent to which environmental variables were associated with certain sets of traits (RLQ analysis), then which specific traits were most strongly selected (fourth-corner method). RLQ analysis (Dolédec et al. 1996) is a multivariate ordination technique that simultaneously considers the information in three tables (R,L and Q). This method extends co-inertia analysis, a two table direct gradient analysis, with the original purpose of characterising species-environment relationships (Dolédec and Chessel, 1994). The RLQ framework was developed on theory based in early community ecology (Whittaker, 1967; Austin, 1968; Keddy, 1992; Southwood, 1977; Palmer, 1993; Southwood, 1977), and driven by recent statistical advances, it is now increasingly used in ecology to assess the relationships between environment, species and traits (Dray and Legendre, 2008; Lacourse, 2009; Brind'Amour et al. 2011; Farneda et al. 2015). In particular, it is useful for identifying syndromes of trait responses across ecological gradients which act to filter meta-community trait diversity (Gámez-Virués et al. 2015). RLQ enables this by using the three original tables of Q ($p \times s$) describing s traits for p species with n samples, R ($n \times m$) with the measurements of m environmental variables in n samples, and L a $n \times p$ table of species abundances (or occurrences) of p species within n samples, to produce the 'fourth-corner' $s \times m$ matrix Ω (Dray et al. 2014). This fourth-corner matrix essentially provides coordinates of sites in multidimensional trait space, consisting of traits weighted by species abundances, and quantification of their associations to standardised environmental parameters (i.e. a trait-environment summary).

To test for environmental selection of traits within this framework, I used the *species* $\times$

trait matrices based on the vegetative and reproductive traits listed in Table A.1. For the R matrix, I used all the environmental variables (listed in Table 2.1) for which I had data in each sample. Furthermore, the recent development of a multivariate test statistic (S_{RLQ}), and improvement of permutation testing procedures (Legendre et al. 1997; Dray and Legendre, 2008; Braak et al. 2012), has enabled a 'global' significance test of trait-environment associations, which I used to test $H_0 : X = 0$ (traits and environment are unrelated) against $H_1 : X \neq 0$ (traits and environment are somehow related).

To carry out the RLQ analysis I extensively relied on the R package **ade4** (Chessel et al. 2004; Dray and Dufour, 2007; Dray et al. 2007). To produce the three tables required for the RLQ procedure I carried out a correspondence analysis (COA, function *dudi.coa*, Borcard et al. 2011) of the species data per site (L) and Hill-Smith analyses of the environmental variables from each site (R) and trait variables per species (Q). The Hill-Smith analysis is an ordination method that facilitates mixing of quantitative variables and factors (function *dudi.hillsmith*, Hill and Smith, 1976). I applied row weighting to the environmental table R with the column weights of table L, and row weighting to the trait table Q with column weights of L to provide standardisation. The resulting tables were then passed to the function *rlq* to compute the results. Testing of the global hypothesis was carried out using the function *randtest* with 9,999 permutations of the sequential-testing procedure (discussed further in Section 3.2.2). This process was repeated for each trait data set (vegetative vs. reproductive), as well as for each spatial sub model (discussed in Section 3.2.3).

3.2.2 Bi-variate trait-environment relationships: Fourth-corner method

Fourth-corner analysis is very similar to the RLQ method in that it computes an $s \times m$ matrix Ω. However, the 4th-corner method is implemented to evaluate the bi-variate associations corresponding to the cells of Ω. Dray et al. (2014) use the analogy that "if we consider a table of quantitative variables for which a correlation matrix can be computed, RLQ analysis would be similar to the PCA performed on this table whereas the fourth-corner

method could be related to the correlation tests computed for each pair of variables". In combination, RLQ and fourth-corner methods are able to provide a wealth of information pertaining to environment-trait associations. Examples of their use includes objectively identifying ecologically informative traits (Bernhardt-Römermann et al. 2008; Dray et al. 2014) and assisting species distribution modelling (Pakeman, 2011), as well as linking traits to ecosystem functioning (Pedley and Dolman, 2014; Spitz et al. 2014; Pease et al. 2015) and management (Ikin et al. 2012; McManamay et al. 2015).

Carrying out the 4th-corner analysis is straightforward using the R package **ade4** (Chessel et al. 2004; Dray and Dufour, 2007; Dray et al. 2007). Initially this procedure permutes the values of sites (i.e. rows of R or L), while holding traits of each species fixed, to test the null hypothesis that the distribution of species is not influenced by the environment. Conversely, the alternative hypothesis considers that the environment does influence the distribution of species. If the null hypothesis is rejected, p species are then permuted (i.e. rows of Q or columns of L) to test the null hypothesis that species composition of samples with fixed environmental conditions is not influenced by the species traits, which are shuffled in the permutation procedure. The alternative hypothesis considers that the traits influence the composition of species assemblages found in samples with given environmental conditions. All tests were carried out with an alpha significance level of 0.05 and false discovery rate p-value adjustment (Benjamini and Hochberg, 1995; Benjamini and Yekutieli, 2001) applied globally.

3.2.3 The combined fourth-corner procedure

When a large number of species, traits, and environmental variables are analysed using the RLQ method, the resulting plots can be hard to interpret due to overcrowding. Similarly, the large number of statistical tests of the 4th-corner method can be hard to summarise. Therefore, Dray and Legendre, (2008) suggest to combine the two methods' testing procedures and carry out fourth-corner testing directly on the RLQ analysis, thus avoiding the a

posteriori combining of the two analyses.

Following these recommendations of Dray and Legendre, (2008), I performed the RLQ analysis and carried out the 4th-corner testing. However, I use the tables produced from the RLQ method as variables for the 4th-corner instead of the original data tables (i.e. tables R^* and Q^*). I used the modified permutation model to test the uni-variate associations of both R with Q^* and Q with R^*. I then estimated the p-values of each model by comparing the observed statistic (S_{RLQ}) to the permuted distribution. For each significant uni-variate association, I used the maximum p-value and applied an adjustment for multiple testing. This resulted in clearer representation of significant associations between the RLQ analysis and trait and/or environmental variables (Dray and Legendre, 2008).

3.2.4 Spatial scaling in environmental selection for traits: MEMs and the combined fourth-corner

As discussed in both Section 3.1.1.1 and Section 3.1.3.2, MEMs are templates of spatial structuring within the data they are computed from, and sub models of MEMs are linear models pertaining to a given scale. In addition to acting as a template for the structure of spatial autocorrelation they can also be for spatial filtering (Griffith, 2010). Spatial filtering mathematically manipulates data in order to correct for potential distortions introduced by arbitrary scale, resolution, and zonation (i.e. surface partitioning). In this application, the term 'filtering' indicates that the desirable structural features of the original source pass through a "filter", while the undesirable features caused by spatial structuring are blocked. Therefore eigefunction-based methods (i.e. MEM sub models) provide a means to predict environmental conditions within and across multiple spatial scales associated with the spatial configuration they represent, while reducing geographically structured noise from the data and increasing the soundness of statistical inference (Overmars et al. 2003; Miller et al. 2007; Griffith, 2010; Boria et al. 2014). More specifically, MEMs can be introduced to regression models as functions to emphasise and predict environmental values at a given site, which can

then be used as an integrated means to test trait-environment relationships at the relevant spatial scale (Griffith and Peres-Neto, 2006).

I therefore used the defined MEM sub models (Section 3.1.3.2) to model environmental variables at discrete spatial scales. This enabled incorporating a spatial aspect to the combined 4th-corner framework. In doing so, I was able to summarise and test trait-environment relationships at scales relevant to the data set and at which the strongest spatial patterns in species and trait diversity were apparent. To do this I used the eigenvector sub models as predictors of each environmental variable in simple linear models. I fitted a normal regression model for each continuous environmental variable, whereas I created binary dummy variables for categorical ones and fitted a logistic model for each. I then created a table of new environmental values ($\hat{R}$) for each variable at each site using the fitted values from each model. This was carried out for the environmental data at each spatial scale (i.e. broad/regional and fine/landscape) and used as the environmental variables in subsequent RLQ and 4th-corner analysis. The results were then interpreted as per in previous sections.

Chapter 4

Results: How do environmental drivers of change influence community species and trait composition?

4.0.1 Summary

This chapter presents the results of analyses used to investigate how environmental drivers of change influence community species and trait composition. I present the results in three sections. I first present the results of the combined RLQ-4th-Corner analyses, which were used to explicitly characterise and test multivariate and univariate vegetative and reproductive trait-environment relationships. I then present the results of the spatial modelling. Morans Eigenvector Maps selection was used in combination with ordinations to investigate and summarise patterns of biodiversity in the study area, and then used as spatial filters to account for, and create templates of, the measured environmental variables driving the the observed structural patterns. Finally, I present the results of the multi-scale combined RLQ-4th-Corner analysis, which was used to illustrate how the importance of trait-environment relationships may vary between landscape and regional scales.

4.1 Environmental selection of species and traits

4.1.1 Global assessment of environment, traits and species covariance: RLQ analysis

The RLQ analyses highlighted the nature of a three-way relationship between species, environment and traits for the analysed sampling period (2000's). The RLQ analyses also characterised strong environmental gradients, patterns in species community organisation, and identified trait syndromes (i.e. groupings of traits). For both vegetative and reproductive trait data, the first axis of the *RLQ* analysis preserved greater than 79% of trait variance, while the variance explained by the second axis was typically low ($8 - 10\%$) (summary statistics for each analysis are presented in Table B.1 & Table B.2). The trait—environment correlations were consistently moderate and weak for the first and second axes respectively. Variance from the two table ordinations (Hill-Smith and Correspondence analyses) incor-

porated into the first two axis of the *RLQ* analysis was highly preserved for environmental scores but only moderately for traits. This means that the analysis was only able to account for the strongest trait-environment relationships of the data. Variance in reproductive traits was higher than that of vegetative traits across the study period (difference in variance was 0.205). Monte-Carlo tests applied to evaluate the global traits-environment relationships, based on the total inertia of the RLQ analysis, were highly significant ($p < 0.01$) for both trait datasets (Figure B.3). Thus, I was able to reject the null hypothesis that community traits were not determined by any of the measured environmental variables. Therefore, the environment selects both for traits (independent of species), and also for species, independent of the traits for which I have measured (although likely driven by other unmeasured traits also).

The first axis of the *RLQ* analysis of the vegetative traits (Figure B.1) appears to identify species and traits across a gradient of land use, such as herbaceous annual and biennial species (e.g. *Veronica* sp., *Vicia sativa*) on the left. These species were mostly found in locations with chemically reduced soils (Gley) of high water availability (Saturation), greater monthly mean temperatures and a greater proportion of exotics species in the community. The right side identified plants of lower and spreading stature including grass-like plants, small ferns and prostrate shrubs associated with soils of greater chemical stability (Brown soils and greater CEC), increased precipitation and higher elevation. These locations tended to have previously been under a grazing regime and were associated with the species *Isolepis aucklandica*, *Polystichum vestitum*, *Schoenus pauciflorus*. The second axis separates locations on historical land-use regimes and underlying rock type. The positive (top) part of this axis was associated with biennial herbs and mat-forming species (e.g. *Chionohebe thomsonii, Hectorella caespitosa, Gentianella montana, or Veronica pulvinaris*) in locations currently or previously grazed locations on Schist rock. The negative (bottom) part of this axis was associated with previously ungrazed conservation estate and woody-seral or longer-living species (e.g.*Pteridium esculentum, Kunzea ericoides*, or *Cyathia dealbata*).

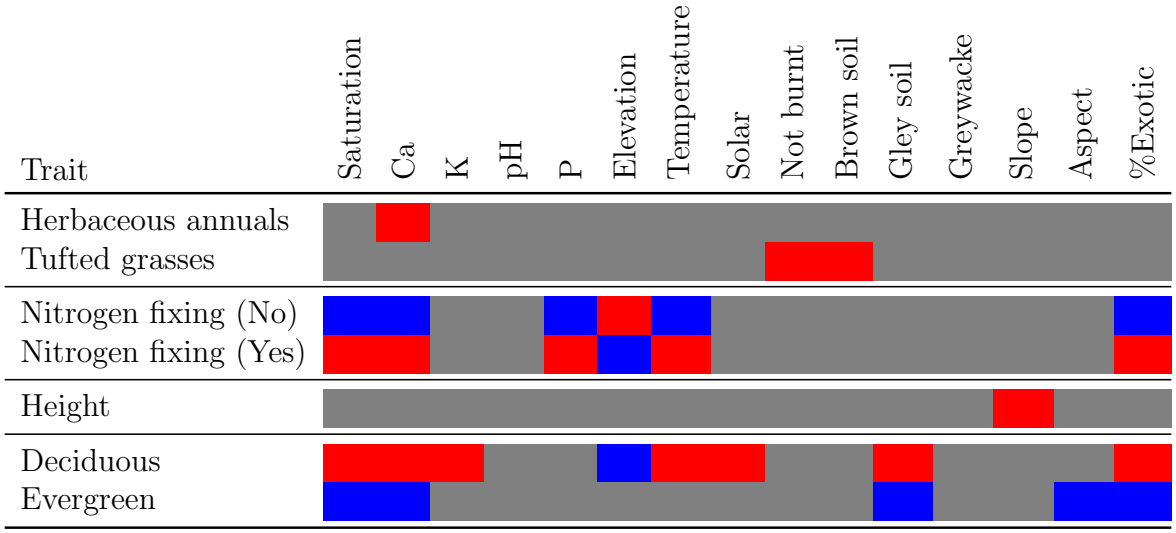
The first and second axes of the reproductive-trait *RLQ* analysis (Figure B.2) appear to separate environmental variables similarly to those of the vegetative trait *RLQ* analysis. That is, species traits were determined land-use on the first axis and physical site properties on the second. However, the interpretation of trait syndromes on the individual axes is less clear. The top-left side of the ordination identifies over-wintering species which flower and fruit later in colder seasons, but in locations which typically experience greater annual temperatures and are more likely to be under pastoral tenure (e.g. *Agrostis* sp., *Bromus tectorum, Rumex obtusifolius*). The top-right side most strongly identifies species (e.g. *Poa* sp.) which reproduce earlier than those previously mentioned, and also possess stoloniferous growth traits. These traits are associated with colder annual temperatures, increasing elevations and the removal of grazing. The bottom of the ordination most strongly identifies species with birds as pollen vectors (e.g. *Phormium cookianum*) and under-ground clonal reproductive traits (e.g. *Rosa rubra* with root suckers). These traits are associated with an absence of grazing and burning, increased slope, and Greywacke rock.

4.1.2 Univariate environment trait associations: Fourth Corner Analysis

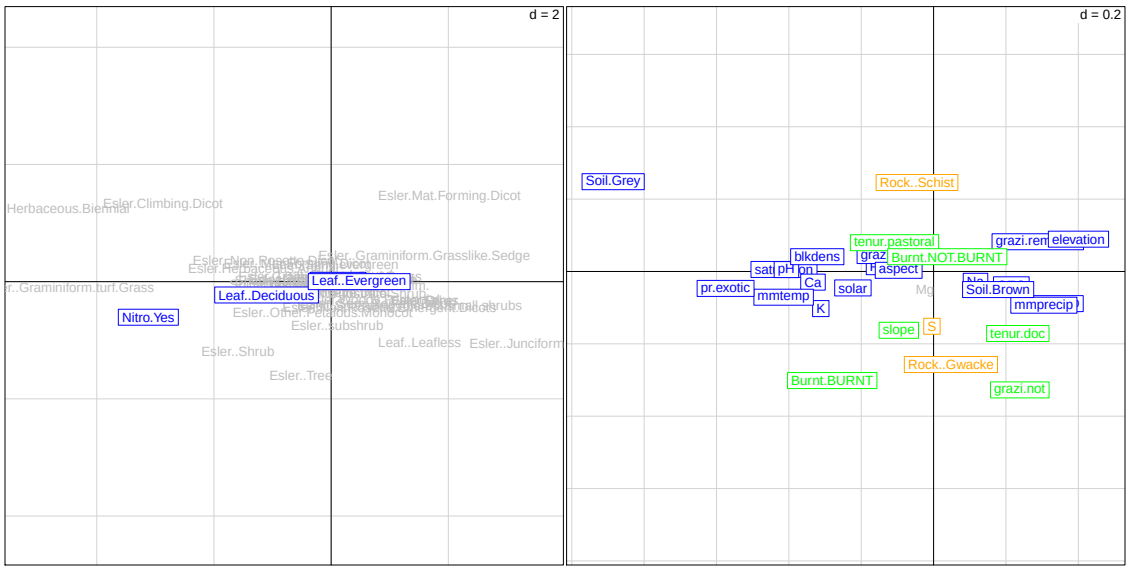
4.1.2.1 Vegetative traits and environmental associations

The 4th-corner univariate analysis highlighted several highly significant vegetative trait-environment associations. Significant trait-environment correlations are shown in Table 4.1. Nitrogen fixing and deciduous traits showed the greatest number of significant correlations, most of which were with physio-chemical environmental variables (e.g. soil variables and climate), as well as the proportion of exotic species in a community. Herbaceous annuals and tufted grasses (i.e. tussocks) also showed significant correlations, however these were fewer, and associated with soil variables and burning. Tufted grasses were the only trait to respond to land-use variables.

Table 4.1: The results of the vegetative trait fourth-corner analysis. Significant positive trait-environment are shown in red and negative shown in blue (grey shows no association). All associations are significant to $P < 0.01$ and were tested with 9,999 permutations and false detection rate p-adjustment applied. Trait and environmental variables with no significant associations are not presented.



Combining the *RLQ* and 4th-corner methods, to test trait-environment relationships using the *RLQ* axes, resulted in a loss of significant associations compared to each analysis carried out on its' own(Figure 4.1). This likely resulted from the weak trait—environment correlations between the second axes (shown by an absence of significant traits on the second axis). Carrying out these analyses in this way largely highlighted the previous dominant and significant relationships between nitrogen fixing capabilities, deciduous plants and environmental variables. Both of these traits were significantly associated with the first axis of the environmental variables. Nitrogen fixing and deciduous traits were most strongly associated with gley soils and an increased percentage of exotic species in the community. In contrast, traits associated with nitrogen fixing or being an evergreen plant were associated with an increased elevation, removal of grazing, and increased precipitation.



(a) Traits **(b)** Environment

Figure 4.1: Vegetative trait and environment factorial maps. *RLQ* scores are used to represent (a) traits and (b) environmental variables for each plot and significant associations revealed by the 4th corner analyses are coloured. Significant associations with the first axis are shown in blue, with the second axis orange, with both axis in green (variables with no significant associations are greyed). Significance was assessed at $\alpha = 0.05$, with 9,999 permutations and false detection rate p-adjustment applied.

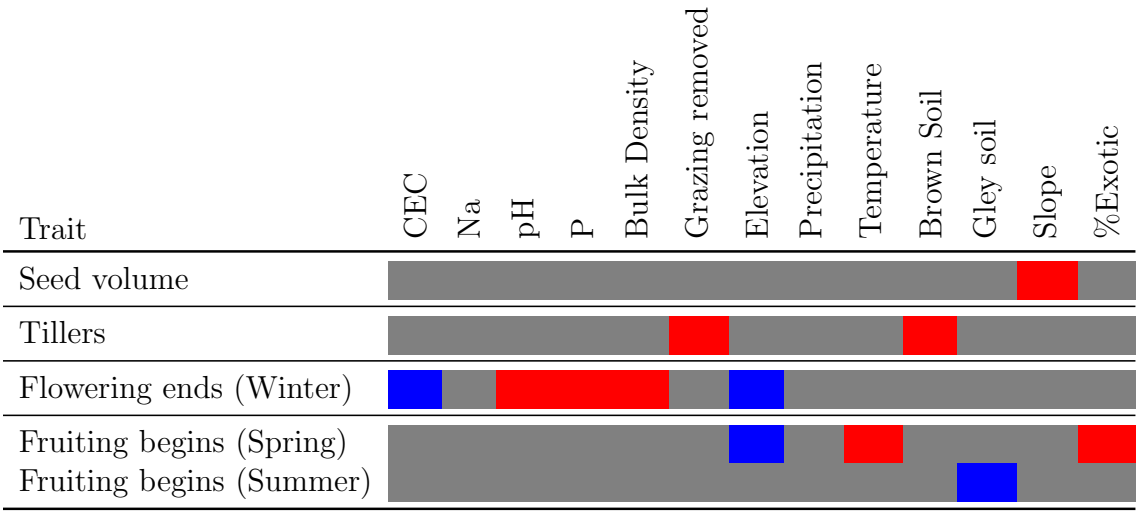
4.1.2.2 Reproductive traits and environmental associations

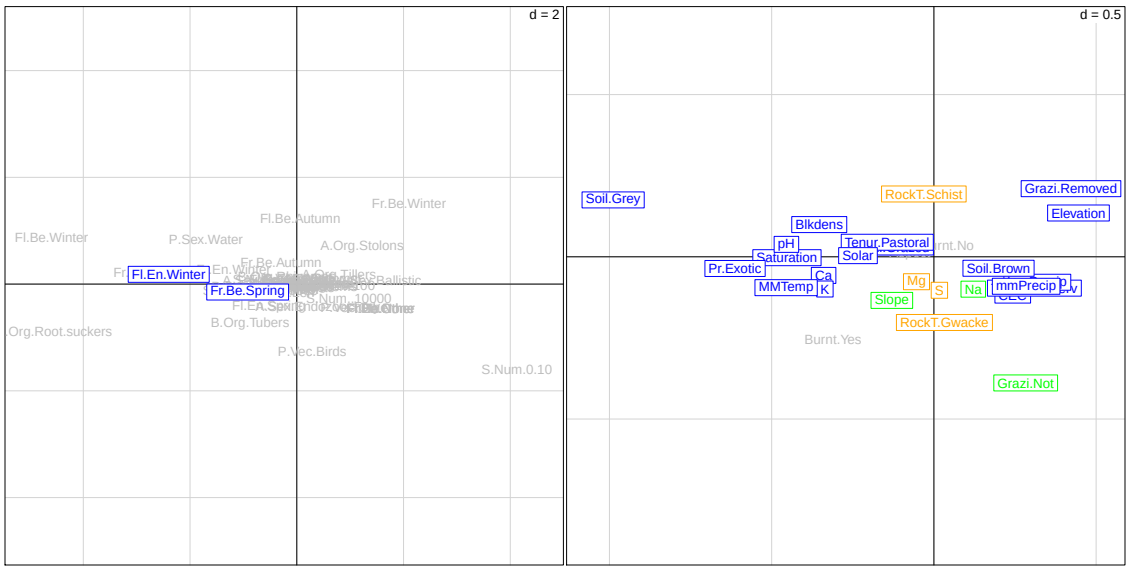
The 4th-corner univariate analysis highlighted fewer significant reproductive-trait-environment associations in comparison to that of vegetative traits (Table 4.2), and these were also of decreased significance ($p < 0.1$). This is most likely the result of increased variance present in the reproductive trait data. Flowering ending in winter showed the largest number of significant environmental associations, mainly with soil-related variables. Seed volume was positively associated with site slope, as were tillers with brown soils and the removal of grazing. Fruiting beginning in spring showed positive associations with increases in temperature and the proportion of exotic species present in the community, and a negative relationship with increased elevation. Fruiting in summer, however, only showed one significant relationship, and that was negative with gley soils.

The combined *RLQ* 4-th corner procedure showed flowering ending in winter and fruiting begining in spring as significant ($p < 0.05$). These traits were associated with the left side

of the first axis of the environmental variables (Figure 4.2). As with vegetative traits, this section of the axis was associated with gley soils, an increased proportion of exotics present and the presence of grazing. No other traits were shown to be significant.

Table 4.2: The results of the reproductive trait fourth-corner analysis. Significant positive trait-environment correlations are shown in red and negative shown in blue (grey shows no association). All associations are significant to $P < 0.1$ and were tested with 9,999 permutations. Traits and environmental variables with no significant associations are not presented.





(a) Traits **(b)** Environment

Figure 4.2: Reproductive trait and environment factorial maps. *RLQ* scores are used to represent (a) traits and (b) environmental variables for each plot and significant associations revealed by the 4th corner analyses are coloured. Significant associations with the first axis are shown in blue, with the second axis orange, with both axes in green (variables with no significant associations are greyed). Significance was assessed at $\alpha = 0.05$, with 9,999 permutations and false detection rate p-adjustment applied.

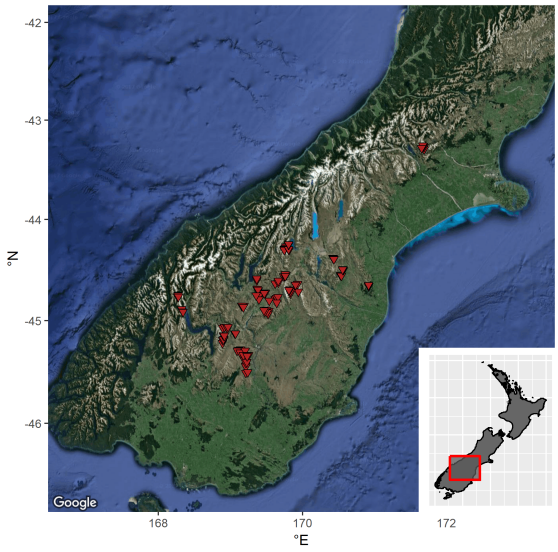
4.2 Spatial and environmental structuring of species and traits

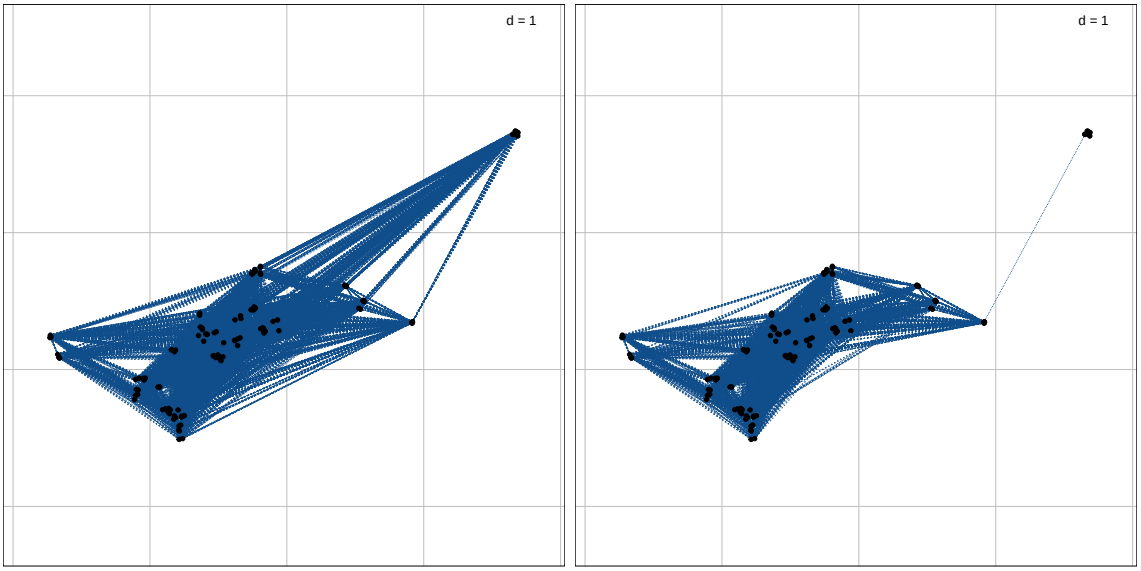
4.2.1 Classification of global spatial models: MEM model selection

The above results collectively demonstrated that environmental variables shaped the community composition of vegetative and reproductive traits. However, some of this variation could be explained by spatially correlated patterns of environmental conditions. I therefore explored the variation in community, species and trait composition that could be jointly explained by spatial patterns independent of, and combined with, environmental influences.

The variance of species and trait composition was decomposed with respect to significant positive and negative Moran's eigenvector maps (MEMs). MEMs were computed in several

steps for community species and trait composition. Ten networks of neighbourhood by Euclidean distances were calculated for each community species and trait dataset and the network of best fit was selected by the lowest $AICc$. For both species and reproductive-trait datasets, the threshold distance within which sites were considered neighbours was 324.962 km, however, the distance for vegetative traits was 155.4 km (For AICc values see Table C.1). The resulting network maps are presented in Figure 4.3. Sites considered neighbours had the greatest number of connections in a North–South pattern and were clustered in the centre of the study area, with fewer connections following the West–East gradient. The second step involved weighting the network by selecting and applying the best distance decay function. The best distance decay power of 9 functions, as selected by $AICc$, was consistent across all datasets (Table C.2). The function selected to be applied as weights to each of the network links was concave down, $1 - (D/D_{max})^3$, where D is the distance of the link between sites and D_{max} is the distance threshold. The best MEM models for each dataset were then used to identify the spatial structuring of community composition and environmental variables relevant to either local or regional spatial scales (presented in Section 4.2.3).





(a) Species and reproductive trait site network

(b) Vegetative trait site network

Figure 4.3: Site connection networks used for calculating Moran's Eigenvector Maps for (a) species and reproductive traits and (b) vegetative traitssets. The original study site map is given as reference (top). The first network (a) was identical for species and reproductive traits (D_{max} = 324.962 km). The vegetative trait network (b) has a lower connection distance threshold distance (D_{max} = 155.4 km). Connections networks are based on a best Neighbourhood by Euclidean distance function selected by an $AICc$ model selection procedure. d (top right) indicates the distance of the grid (grain), one grid square = 100 km.

4.2.2 Environmental and spatial structuring in species and trait diversity

The ordinations of species and community trait composition both indicated spatially induced structuring at multiple scales before and after accounting for environmental effects. Maps with projected site scores for each analysis, associated scalograms showing significant eigenvectors, and environmental correlations are given in in the presentation of each dataset results. Tabular summary statistics for each analysis are given in Table C.3. Variation partitioning of community composition in response to environmental and spatial variables showed that negative spatial autocorrelation had a much greater effect in structuring trait than species composition. Graphs of variation partitioning contrasting positive and negative eigenvectors are shown in Figure 4.6, while those showing scale-specific negative autocorrelation in trait composition are shown in Figure 4.10. The analyses for each species and trait data set are discussed below.

4.2.2.1 Species composition

The first two axes of the PCA of the species data cumulatively captured 29.1% of the variation in community species composition (Top row, Figure 4.4). The scalograms (inset on each ordination, Figure 4.4), which assess the significance of R^2 values using Monte-Carlo permutation testing, for these two axes showed important and significantly non-random MEM groups ($p = 0.001$). This indicates both positive and negative spatial autocorrelation in species composition at broad-scales.

The environmental variables, introduced by the RDA, explained a significant proportion of variation of the initial PCA (R^2=0.498, P=0.001 based on 999 permutations) (Middle row, Figure 4.4). A total of five axes attributable to environmental variables were required to account for 71.14% of the total variation in species composition. The first two axes explained 32.6% and 17.1% , respectively, and correlated most strongly with the proportion of exotic species present, physical variables, parent rock type and land-use variables (Figure 4.5a).

The scalograms associated with this ordination showed important variance accumulation on the first axis, from broad-scale negative autocorrelation ($P = 0.005$) through to broad-scale positive autocorrelation ($P = 0.001$). Two groups of MEMs representing broad-scale negative autocorrelation were significantly non-random for the second axis ($P = 0.001$ & $P = 0.005$). This shows the measured environment spatially structured, and this is influencing species composition at broad spatial gradients.

The first two axes of the partial redundancy analysis (variation after accounting for the effect of measured environmental variables) explained 21.067% of the total residual variation. No significant spatial components were found in the residuals, meaning that no spatial patterns remained after the spatial structuring attributable to the measured environmental gradients were partialed out. This shows that some unmeasured spatial processes still influenced species composition (but were captured by the MEMs), however, that the MEMs adequately modelled the environmentally-induced spatial structuring within the data (Bottom row, Figure 4.4).

ANOVAs testing for the global significance of environment and spatial predictors of species composition, prior to variable forward selection, indicated that both predictor groups were highly significant (environment, positive & negative MEMs all $P<=0.001$). The forward selection procedure reduced these sets of variables to 12 environmental variables (Table 4.3), 3 positive eigenvectors and 9 negative eigenvectors. Partitioning of the variation using selected variables showed local environmental conditions had the strongest effect on species composition (Figure 4.6a), accounting for 27% of the total explained variation. Negative spatial autocorrelation was the second greatest effect explaining a total of 16% of the variation, with 11% of this being a shared fraction with environmental variables, and 4% with positive MEMs. The pure positive MEM fraction accounted for only 1% of the variation in species composition.

Table 4.3: Environmental variables included in spatial modelling following forward selection for each community composition data set. Variables are presented in the order in which they were selected by the forward-selection procedure. Forward selection was carried out with a double-stopping criterion of $\alpha = 0.05$ and a R^2 threshold defined by the adjusted R^2 value from an RDA carried out on each data set. Descriptions of each variable are included in Table 2.1.

Species	Vegetative traits	Reproductive traits
%Exotics	%Exotics	%Exotics
Gley Soil	Gley Soil	Slope
Elevation	Greywacke	Saturation
Precipitation	Temperature	Elevation
Greywacke	Conservation tenure	Bulk Density
CEC	Grazed	Solar
Saturation	Slope	Aspect
Not burnt	Elevation	Greywacke
Solar	Saturation	
K	Site aspect	
Mg	Solar	
Not grazed	K	

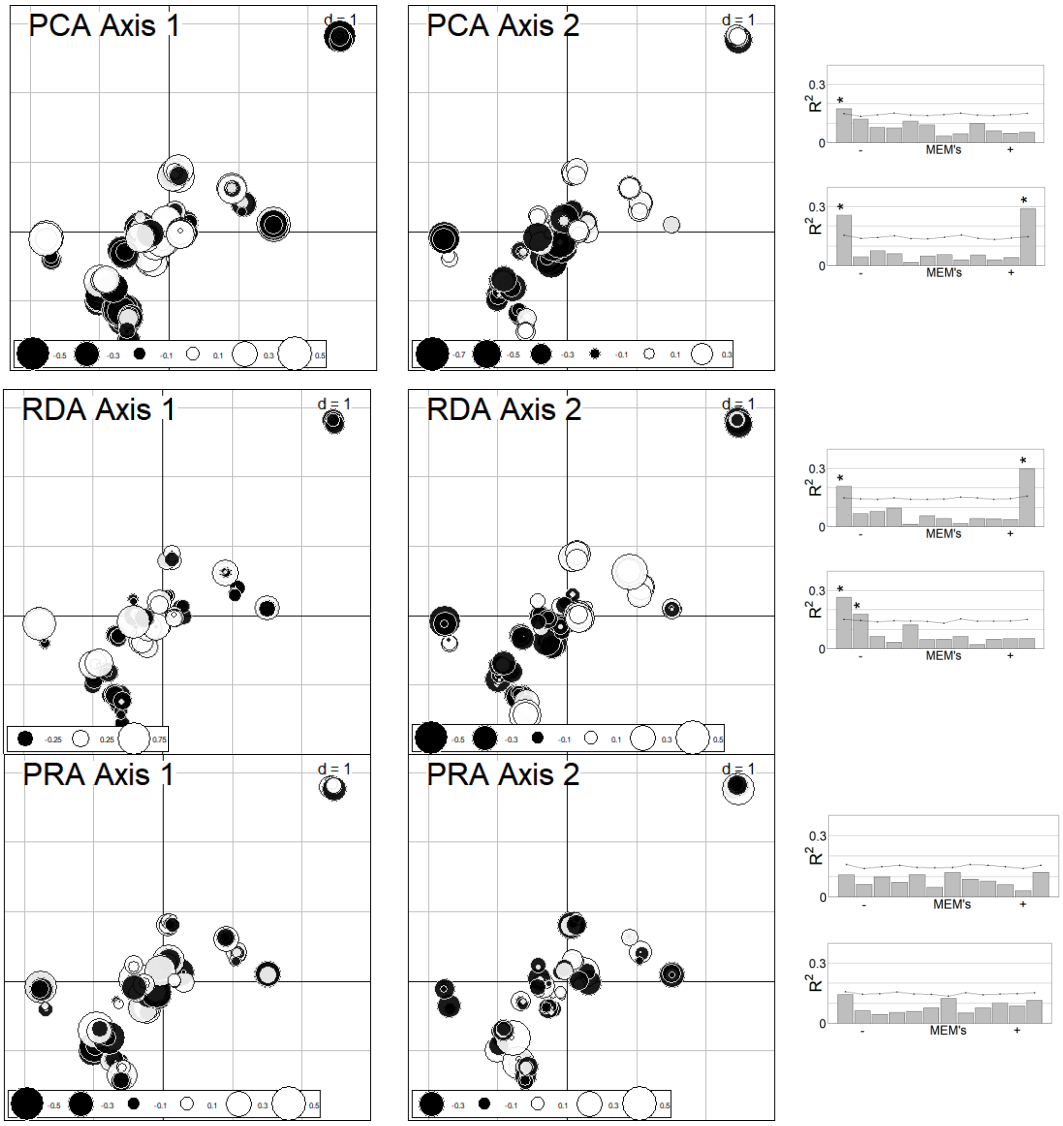
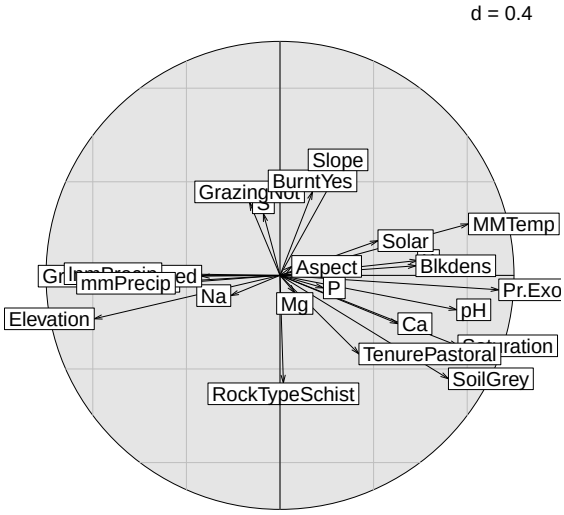
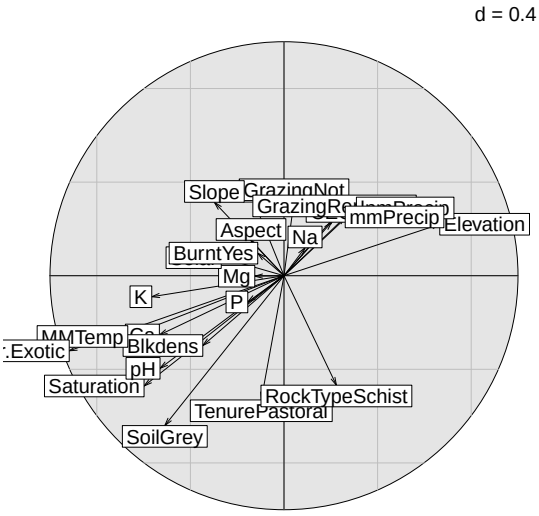


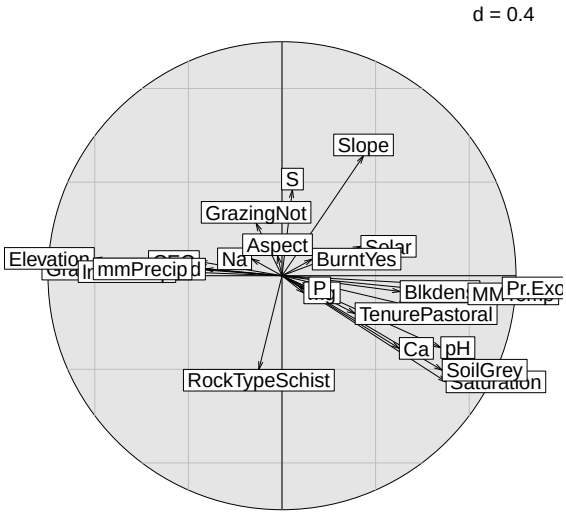
Figure 4.4: Maps of site scores on the first and second axes of the principle component analysis of species composition (top row), the redundancy analysis of species composition with environment variables as predictors (middle row) and the partial-redundancy analysis (with environment as co-



(a) Species

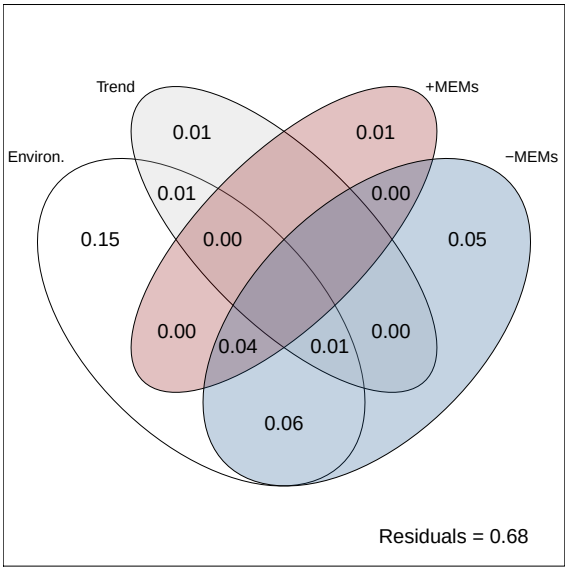


(b) Vegetative traits

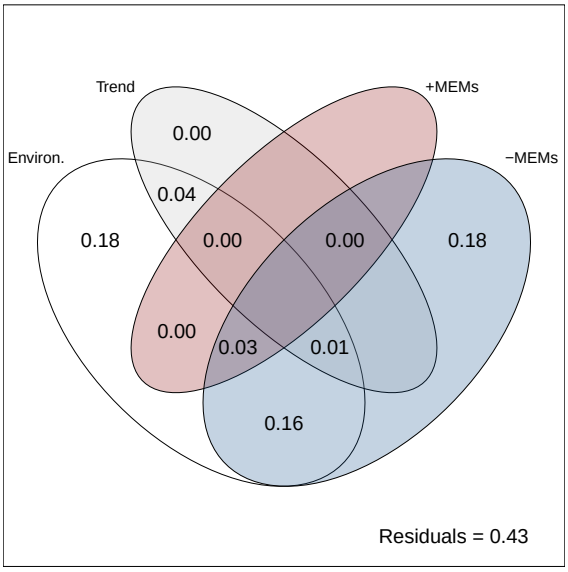


(c) Reproductive traits

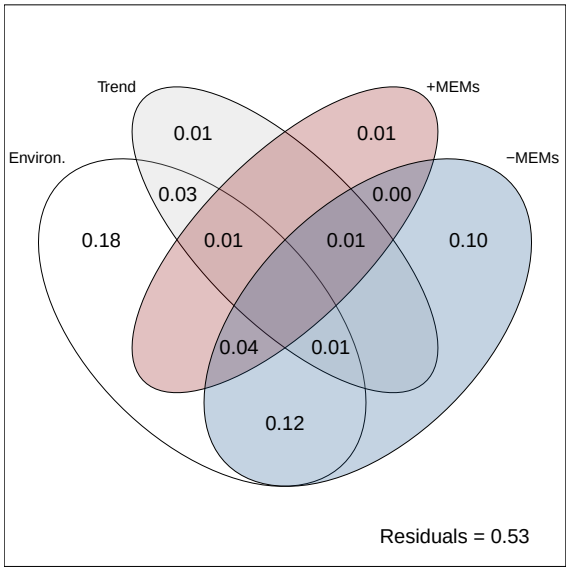
Figure 4.5: Environmental correlations with the first and second axes of the redundancy analysis carried out on species and trait community composition.



(a) Species composition



(b) Vegetative-trait composition



(c) Reproductive-trait composition

Figure 4.6: Adjusted R^2 values for each fraction for the variation partitioning of species and trait composition between forward-selected environmental variables, longitudinal coordinates (trend) and negative and positive Moran's Eigenvector Maps. $R^2 < 0$ are not shown.

4.2.2.2 Vegetative-trait diversity

The first two axes of the PCA of vegetative trait composition cumulatively captured 58.261% of the variation in trait diversity (Top row, Figure 4.7). The scalograms for these plots show important and significant variance accumulation in broad-scale positive MEMs on the first axis ($p = 0.012$), and a series of significant broad-scale negative and positive MEMs the second axis ($p = 0.032$, $p = 0.048$ and $p = 0.04$, respectively, see inset Figure 4.7). The environmental variables explained a significant proportion of variation in trait composition (RDA, $R^2 = 0.741$, $P = 0.001$ based on 999 permutations)(Mid row, Figure 4.7). The first two axes explained 46.66% and 27.43% respectively (Table C.3). The strongest correlations of these axes were with %Exotic species present, soil type, and elevation (Figure 4.5b). The first axis showed significant broad-scale positive MEMs ($p = 0.038$), while the second axis showed significant broad-scale negative MEMs ($p = 0.005$). In addition to this, both axes showed relatively large amount of variance accumulation associated with finer-scaled negative MEMs. However these were non-significant. This shows that the effect of measured environmental variables on vegetative trait composition accounts for much of the finer-scale spatial autocorrelation, but, both negative and positive broad-scale autocorrelation remained unaccounted for by the measured environmental variables.

After removing the effect of environmental variables, the partial redundancy analysis accounted for 51.019% of the total residual variation (Bottom row, Figure 4.7). Significant spatial structuring explained by broad-scale positive MEMs remained in the data. For both axes the tenth group of MEMs was significant ($p = 0.005$ & $p = 0.001$), showing that some spatial driver explained by the MEMs, but not attributable to measured environmental variables, was responsible for structuring the composition of vegetative traits.

ANOVAs testing for the global significance of environmental and spatial variables, prior to forward selection and variation partitioning, were carried out on the community data and included the geographic coordinates of sites as an additional group of spatial predictors. Including site coordinates enabled testing for a linear trend, acting on both community

composition and environmental variables, occurring at a greater scale than the sampling area (i.e. induced spatial dependence; Legendre and Gallagher, 2001). All three groups of predictors were highly significant (i.e. environment, MEMs and site coordinates; $p < 0.05$). Therefore, forward selection and variation partitioning was carried out using the undetrended vegetative trait compositional data. Variation partitioning was able to account for 57% of the variation in trait composition. The 12 selected environmental variables (shown in Table 4.3) explained 26% of this explained variation, 16% of this was a shared fraction with negative MEMs, 4% with latitudinal coordinates, and 3% with positive MEMs. The 22 selected negative MEMs had the second greatest explanatory power ($R^2_{adj.} = 0.38$), with 18% of their explanatory power associated with a pure fraction. The shared environment and negative MEM fraction shows that measured environmental conditions occurring at a scale greater than the site level are driving greater diversity in vegetative trait composition, across sites, than would be expected at random. In addition to this, the pure negative MEM fraction shows that some unmeasured and spatially structured process has a same effect of similar magnitude. The absence of a pure fraction associated with the single positive MEM and the presence of both shared environment—trend and environment—positive—MEM fractions indicates that incorporating the geographic trend into the analysis accounted for the positive spatial autocorrelation shown in the partial redundancy analysis.

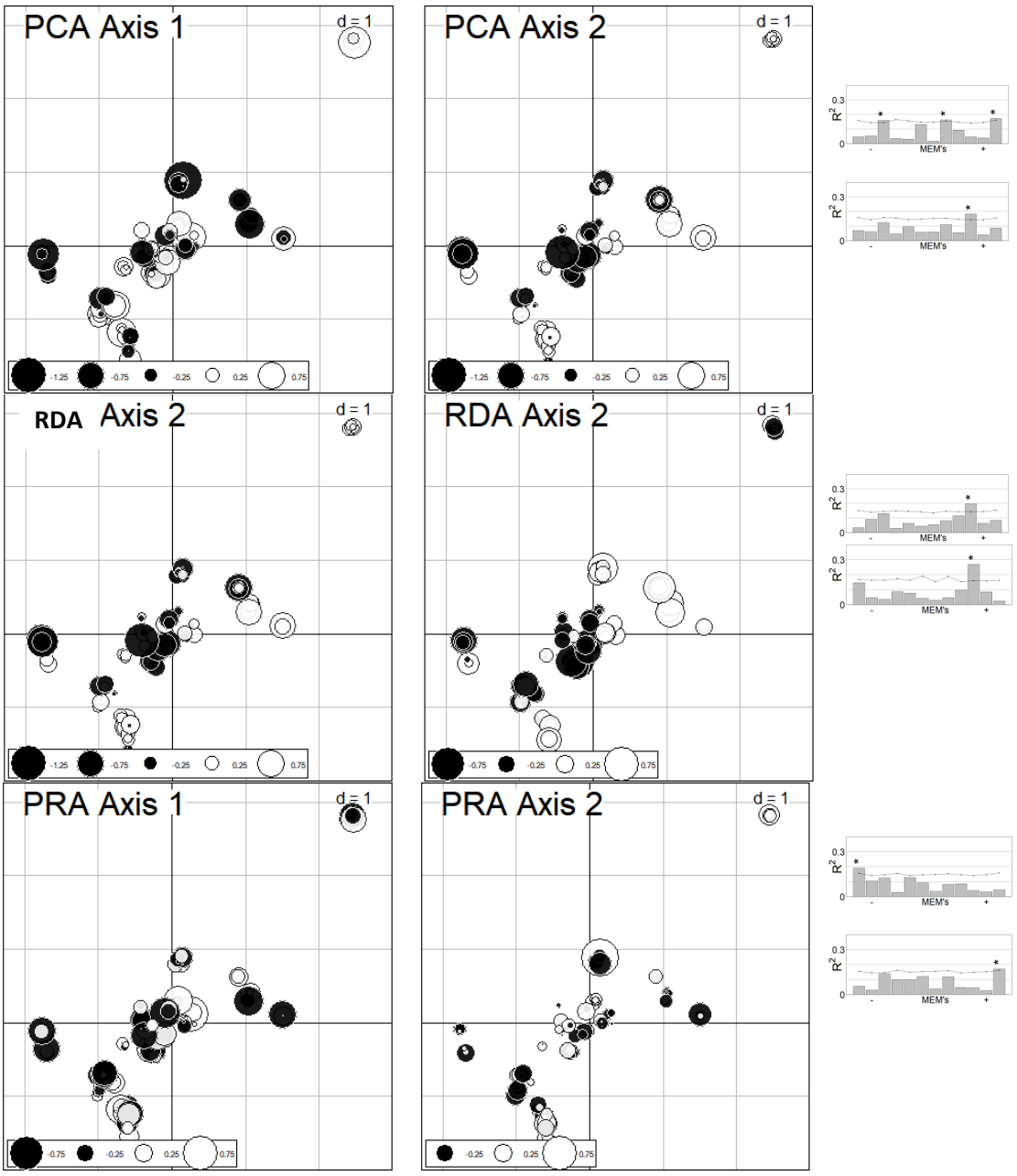


Figure 4.7: Maps of site scores on the first and second axes of the principle component analysis of vegetative composition (top row), the redundancy analysis of species composition with environment variables as predictors (middle row) and the partial-redundancy analysis (with environment as co-

4.2.2.3 Reproductive-trait diversity

The first two axes of the PCA of reproductive trait composition (Top row, Figure 4.8) cumulatively captured 55.506% of the variation in species diversity. The first axis of this analysis showed important and significant associations with both negative and positive MEMs with a broad spatial extent ($p = 0.008$ & $p = 0.001$), while the second axis showed significant negative MEMs over a fine spatial extent ($p = 0.026$). The environmental variables explained a significant proportion of variation in reproductive-trait composition ($R^2 = 0.74$, $P = 0.001$ based on 999 permutations). The first two axes explained 49.59% and 24.42% of the variation within the PCA respectively (mid row, Figure 4.8 & Table C.3). The strength of correlations of these two axes with environmental variables was similar to that of vegetative traits, but showed contrasting distributions along the axes (Figure 4.5c). These two axes also showed very similar components of spatial structuring as shown in the PCA scalograms, that being significant negative and positive MEMs at both fine and broad spatial extents. After removing the effect of environmental variables, the partial redundancy analysis accounted for 43% of the residual variation (bottom row, Figure 4.8 & Table C.3). At this point, only two groups of broad-scale positive MEMs remained significant ($p = 0.022$ & $p = 0.02$). Both of these significant MEMs were associated with the first axis of this analysis. This shows that a large amount of variation in the community composition of reproductive traits, but not all, reflects spatially structured environmental variables. In addition to this, the significant broad-scale positive MEM suggests that some unmeasured spatially-structured variable is responsible for driving spatial trait homogeneity.

Testing of the global significance of environmental and spatial variables (inclusive of site coordinates), indicated that all predictor groups were significant ($p < 0.05$). Following forward selection of these variables, there remained 8 environmental predictors (Table 4.3), 8 MEMs (four negative and 4 positive), and the variable representing the latitudinal site coordinates. Variation partitioning accounted for 47% of the total variation in reproductive-trait composition. The 8 environmental variables explained the largest amount of variation

($R^2_{adj.} = 0.39$), followed by negative MEMs ($R^2_{adj.} = 0.28$). A shared environment and negative MEM fraction accounted for 12% of the total variation and a 4% fraction shared between environment variables and both positive and negative MEMs. A shared environment and trend fraction explained most of the variation associated with the latitude variable (i.e. the induced spatial dependence). Overall, this result was very similar to that for the vegetative traits, indicating that similar processes may be driving the composition of the two.

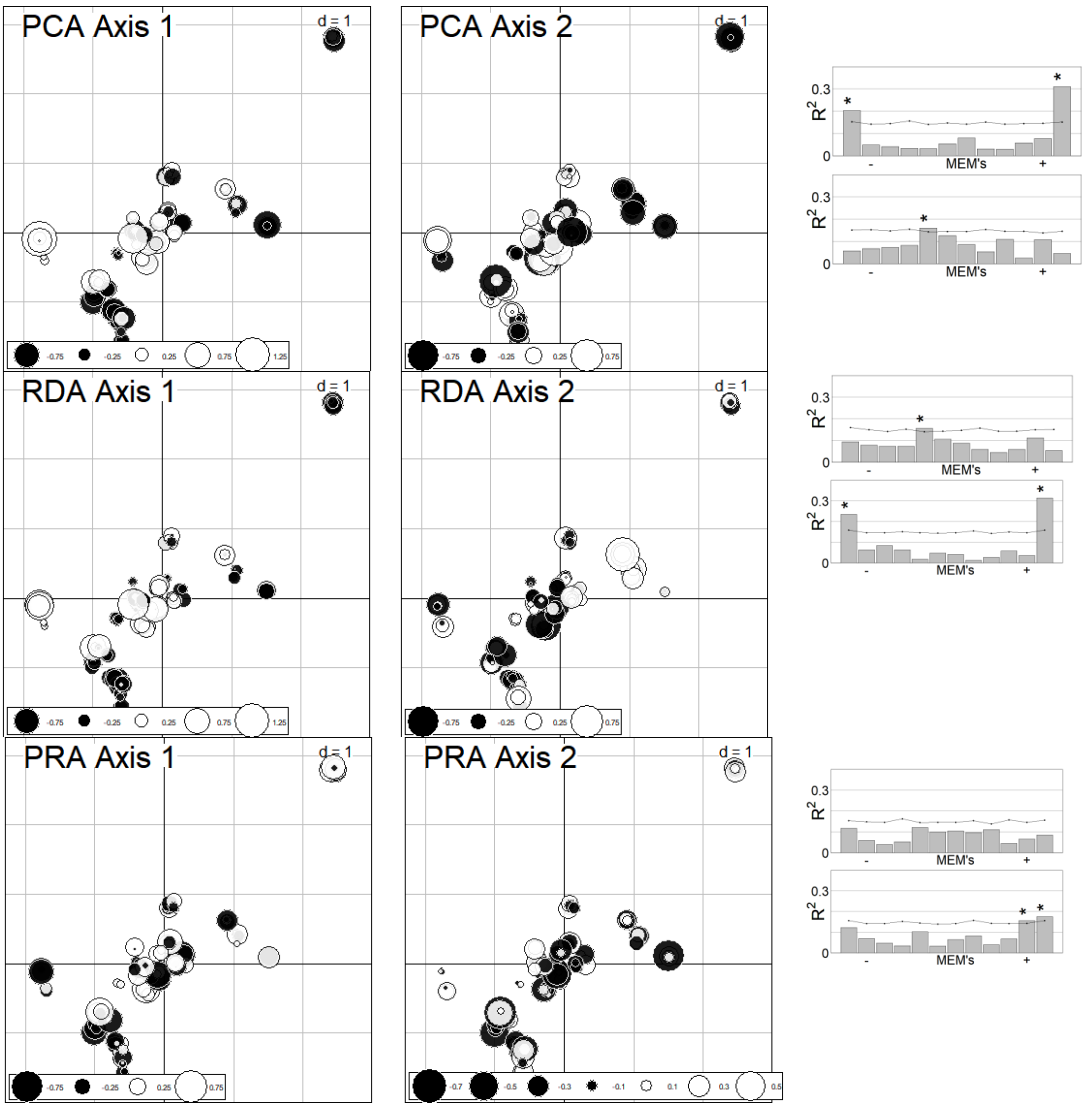


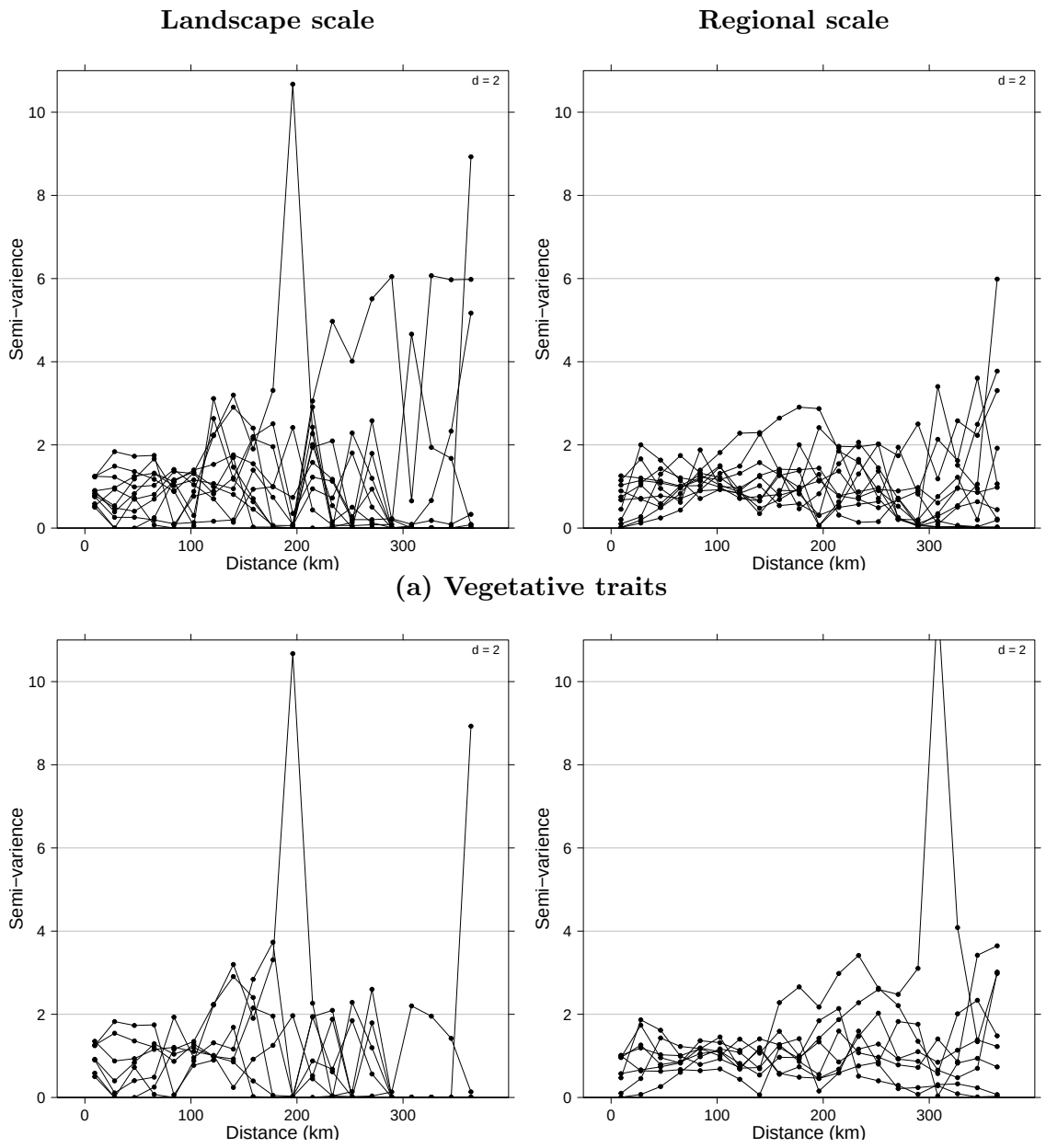
Figure 4.8: Maps of site scores on the first and second axes of the principle component analysis of species composition (top row), the redundancy analysis of species composition with environment variables as predictors (middle row) and the partial-redundancy analysis (with environment as co-variables). For each score, a smoothed scalogram (the 124 Moran's eigenvector maps are assembled

4.2.3 Landscape and regional patterns: MEM sub-model analysis

The variation partitioning of species and trait composition in response to environmental and spatial variables highlighted the strong relative effect of negative spatial autocorrelation. Therefore, to explore the multi-scale spatial influence of trait-environment relationships that drive this increased spatial diversity, I assembled the MEMs showing significant negative spatial autocorrelation into two groups of eigenvectors representing landscape (fine) and regional (broad) scale spatial patterns for each trait dataset. Forward selection of negative eigenvectors reduced the MEMs for each trait data set from 124 eigenvectors to 22 for vegetative traits and 15 for reproductive traits. I defined the two groups of negative MEMs by plotting their semi-variance against distance in kilometres, then allocating each eigenvector (MEM) to either the landscape- or regional-scale groups based on the regularity in the wave each plot formed. These variograms are shown in Figure 4.9. The MEMs I associated with the landscape scale showed an initial reduction in their variance prior to 120 km, and I used that value to delimit this group. MEMs which showed their initial decrease in variance after 120 km were attributed to the regional scale group. To provide additional support for these groupings, I plotted the eigenvalues for each MEM against the site's geographic coordinates (not shown, but similar to those shown for the ordinations). These 'maps' supported the chosen grouping. Fine-scale MEMs showed values clustered together at a landscape scale ($<$ 120km), highlighting 'islands' of distinct trait composition, while broad-scale MEMs highlighted regional-scale patterns in diversity occurring across the entire extent of the study area. Thus, although I acknowledge that the 120km cutoff is arbitrary, it captures broad differences in the data, and its purpose is simply to facilitate the discussion of trends at different scales.

Variation partitioning of environmental variables and MEMs showed similar patterns between the trait datasets. Environmental variables had the most explanatory power for vegetative ($R^2_{adj.} = 0.18$) and reproductive trait composition ($R^2_{adj.} = 0.17$). The variation explained by the shared environment and trend fraction was also identical ($R^2_{adj.} = 0.04$).

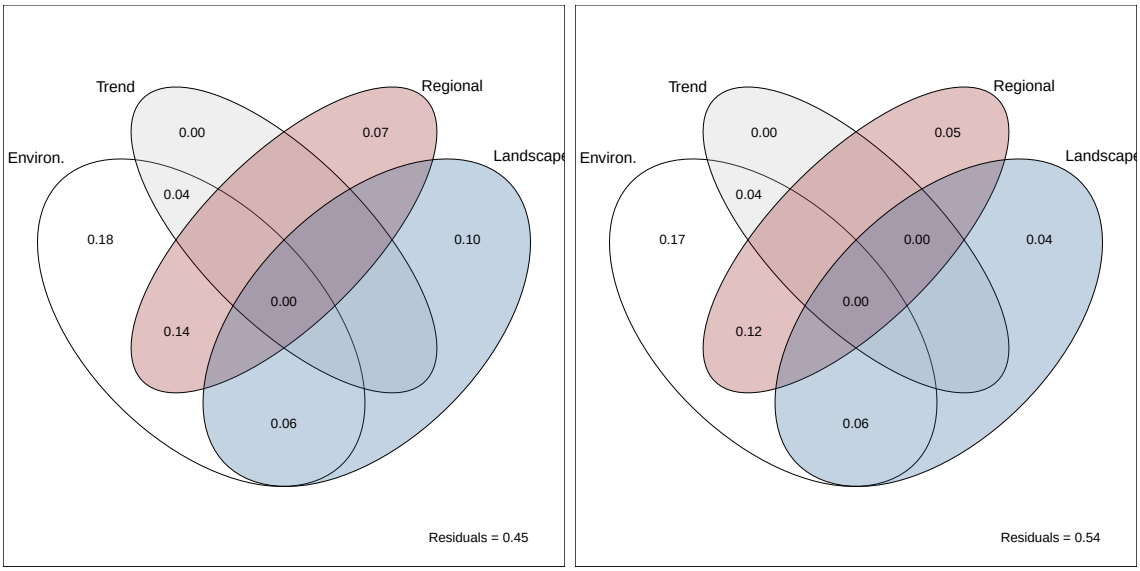
R^2 values of MEMs were marginally greater for vegetative traits than reproductive traits. While the explanatory power of regional scale MEMs was relatively similar between the data sets, the pure landscape-scale MEM fraction for reproductive trait composition was less than that for vegetative trait composition. These results are presented in Figure 4.10. In each case, the large amount of variation associated with MEMs of both scales shows that some unmeasured, and spatially structured, variables are driving an increase in the diversity of vegetative and reproductive trait composition.



(a) Vegetative traits

(b) Reproductive traits

Figure 4.9: Variograms of Moran's Eigenvector Maps (MEMs) for (a) vegetative and (b) reproductive traits. MEMs representing the landscape scale are shown on the left and regional scale on the right. Variograms for landscape scale MEMs of both trait datasets show a sill at approximately 120 km, which was used in conjunction with spatially explicit plots of MEM eigenvalues to delimit the scale which the individual eigenvectors represent and to form the two scale groups.



(a) Vegetative traits **(b)** Reproductive traits

Figure 4.10: Adjusted R^2 values for each fraction for the variation partitioning of trait composition between forward-selected environmental variables, longitudinal coordinates (trend) and landscape and regional-scale negative Moran's eigenvectors. $R^2 < 0$ are not shown.

4.3 Spatial scales in trait-environment relationships

4.3.1 Multi-scale assessment of environment, traits and species covariance: Spatial RLQ analysis

The multiscale *RLQ* analyses highlighted the nature of a three-way relationship between species, spatially-structured environmental variables and traits. The RLQ analyses also characterised strong environmental gradients, patterns in species community organisation, and identified trait syndromes which differed when analysed at landscape and regional scales. For vegetative trait data, the first axis of the *RLQ* analysis preserved greater than 78% of trait variance at both scales (Table D.1 & Table D.2). The second axis preserved only 6.9% of the variance at the landscape scale, but greater than double that at the regional scale (17%). The preserved variance for the first axes of the reproductive traits was higher than that for vegetative traits at both scales (85% & 87.6%), but the total variance for reproductive traits was lower (see Table D.3 & Table D.4). The trait—environment correlations were consis-

tently weak (r<0.3) for the first and second axes of both data sets. Variance from the two table ordinations (Hill-Smith and Correspondence analyses) incorporated into the first two axes of the *RLQ* analysis was highly preserved for environmental scores but only moderately for traits. This means that the analysis was only able to highlight the strongest gradients in the trait data, which was a very similar result to the global analyses (Section 4.1.1). Monte-Carlo tests applied to evaluate the spatial trait-environment relationships, based on the total inertia of the RLQ analyses, were significant ($p < 0.05$) for both trait datasets at both scales, although the significance was slightly greater for vegetative traits (Figure D.3). Thus for all cases, I was able to reject the null hypothesis that community traits were not determined by any of the measured environmental variables. Therefore, the environment selects both for traits (independent of species), and also for species, independent of the traits for which I have measured. Moreover, this relationship holds true when using spatially-filtered environmental variables, chosen to reflect landscape-scale (<120 km) and regional-scale (>120 km) drivers of increased diversity in community trait composition.

Landscape versus regional-scale *RLQ* analyses of vegetative traits differed in their distribution of traits, species and environmental scores along the each axis. At the landscape scale, the strongest gradient along the Y axis was driven by the land-use variables (Figure D.1a). Specifically, the opposing land-use types of previously grazed conservation estate and currently grazed pastoral land. Exotic herbaceous biennials such as *Verbascum virgatum* and *Carduus* sp. formed communities with native early-successional tree species (e.g. *Kunzea ericoides, Leptospermum scoparium*) in the former land-use type, and exotic pasture species were associated with the latter (e.g. *Poa annua, Vicia sativa, Veronica pulvinaris, Hectorella caespitosa*). The x axis formed a gradient across environmental variables associated with changes in elevation. Specifically, with an absence of grazing at high elevations, native-dominated and lower-stature woody communities assembled, in contrast to lower elevations where graminaceous exotic communities dominated. The regional scale showed a similar pattern of traits across the y axis, however with more emphasis on contrasting woody

and graminaceous communities (Figure D.1b). Soil and bed-rock types showed the strongest environmental gradients across this axis. Environmental variables on the x axis highlighted a gradient of lower elevation exotic-dominated communities on the left and previously grazed sites at increased elevation with a lower proportion of exotics on the right.

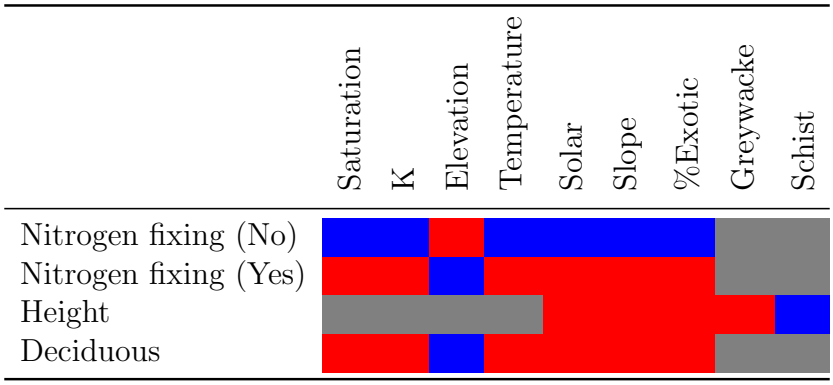
When considering the landscape and regional-scale analyses for reproductive traits, despite slightly different arrangement, there was very little difference between trait and environmental scores on each axis between scales. In both cases, bed-rock type formed the strongest gradient on the environmental variable y axes, with schist at the top (positive) and greywacke at the bottom (negative) (Figure D.2a). These variables were associated most strongly with traits of late-season flowering and fruiting phenologies on the positive side of the axes and species which depend on bird pollination and produce few seeds on the negative. For the x axes, elevation showed a positive score, while physiochemical variables and proportion of exotic species showed negative scores. Lower elevations were associated with warmer fruiting seasons and below-ground clonal reproduction types, while higher elevations showed associations with above-ground clonal reproductive types (e.g. stolons) and a greater number of seeds per plant (Figure D.2b)

4.3.2 Multiscale environment-trait associations: Fourth Corner Analysis

4.3.2.1 Vegetative trait–environment associations

The multiscale fourth corner analysis of vegetative traits highlighted very few significant relationships. However, directly testing the axes of the *RLQ* using the fourth corner method did uncover trait—environment relationships not present in the global analysis. The initial univariate fourth corner results for regional-scale patterns are presented in Table 4.4. Nitrogen fixing, height, and leaf longevity traits showed significant positive and negative associations with the spatially-filtered environment variables. There were no significant univariate

Table 4.4: The results of the regional-scale vegetative trait fourth-corner analysis. Significant positive trait-environment correlations are shown in red and negative shown in blue (grey shows no association). All associations are significant to $P < 0.01$ and were tested with 9,999 permutations and false detection rate p-adjustment applied. Trait and environmental variables with no significant associations are not presented.



trait—environment associations at the landscape level. Using the combined *RLQ*–Fourth-corner method did reveal significant associations at this scale, however (Table 4.5). Only the first axis showed significant associations. At the landscape scale these new relationships were spreading to erect small shrubs and leaf length with the first environmental axis, upon which a number of environmental variables were significant. Nitrogen fixing and leaf longevity were the only traits to show significant associations with environmental axes at the regional scale in the combined analysis.

Table 4.5: Results of multi-scale combined *RLQ*–Fourth-corner analysis of vegetative traits results. (a) Shows the significant associations of traits to the environmental-*RLQ* axis (R), tested using the 4th-corner method (α<0.05), and (b) the significance of environmental variables to the trait-*RLQ* axis. Colours indicate positive (red) or negative (blue) correlations and ordination scores simultaneously. The second axes and non-significant variables are not presented.

(a) Trait—Environment axis correlations

Landscape scale

	Axis R1
Herbaceous annual	
Woody perennial	
Spreading to erect small shrub	
Leaf length	

Regional scale

	Axis R1
Nitrogen fixing (No)	
Nitrogen fixing (Yes)	
Deciduous	

(b) Environment—Trait axis correlations

Landscape scale	Saturation	K	Elevation	Temperature	Solar	Slope	Aspect	%Exotic	Grazed	Not grazed	Conservation	Pastoral	Brown soil	Gley soil	Greywacke	Schist
Axis Q1																

Regional scale	Saturation	K	Elevation	Temperature	Solar	Slope	%Exotic	Grazed	Grazing Removed	Brown soil	Gley soil	Greywacke	Schist
Axis Q1													

4.3.2.2 Reproductive trait–environment associations

Three reproductive traits showed significant environmental associations using the univariate forth-corner analysis. At the landscape scale, these were a constrasting relationship between unspecialised seed dispersal and water dispersed seeds with the two bedrock types. The former trait was positively associated with schist and negatively with greywacke, and the latter showed the opposite associations. At the regional scale, flowering ending in summer showed a positive association with soil saturation, bulk density and the proportion of exotic species present. No traits showed a significant result when directly testing associations with the *RLQ* environmental axes at the landscape scale. At the regional scale, flowering ending in summer was significantly associated with the first axis of the *RLQ* environment axes. This association with environmental variables is show in Table 4.6.

Table 4.6: Results of multi-scale combined *RLQ*–Fourth-corner analysis of reproductive traits (Axis Q1). The table shows the significant associations of flowering ending in summer to the environmental-*RLQ* axis (R) at the regional scale, tested using the 4th-corner method (α<0.05). Colours indicate positive (red) or negative (blue) correlations and ordination scores simultaneously. The second axes and non-significant variables are not presented.

	Saturation	Bulk density	Elevation	Solar	Slope	%Exotic	Greywacke	Schist
Axis Q1								

Chapter 5

Methods: Does the change in abundance of species depend on trait uniqueness and originality (competition) or distance from the optimal community traits (environment)?

5.0.1 Summary

This section details the analytical methods for testing hypotheses pertaining to changes in the relative difference of species abundance between two time periods in response to components of functional trait diversity. Specifically, I test whether species with traits that differ from others in the community increase in relative abundance because of reduced competition (due to low niche overlap). Then I test whether this reduced niche overlap with the community comes at a cost of being a poor fit to the environment, by using the community data from the previous section, to determine if a species' distance from the trait combinations that would be optimally matched to the environment. To answer these questions, I use a mixed-effects modeling framework to test whether the change in abundance of each species from one sample period to another can be predicted by three trait metrics. These are: 1) trait originality (Pavoine et al. 2005), 2) trait uniqueness (Buisson et al. 2013), 3) and distance from trait optimum (Muscarella and Uriarte, 2016). The first two metrics can be used to indicate how an individual species' traits fall within the community trait hyperspace, and thus they serve as a proxy of niche overlap and intensity of competition. The third metric indicates the strength of environmental selection of traits for each species within a given community. This metric was devised by Muscarella and Uriarte, (2016) to test whether community-weighted means (i.e. plot-level trait values weighted by species abundances) and environmental conditions reflect selection towards locally optimal phenotypes (the 'CWM-optimality' hypothesis). I use this metric to specifically contrast the relative effects of trait-based competition vs. the environmental selection of traits. This work compliments the previous chapters, which looked at the environmental influences on species and their traits, by looking at how those traits affect the population trajectories of species.

In this section I outline each of the metrics in turn. I present theory underpinning each metric, explain how they are calculated and justify their use by providing examples. I then outline the methods surrounding the mixed-models used to relate these metrics to the change in abundance of each species.

5.1 Functional diversity metrics

5.1.1 Trait Originality and Uniqueness

Trait originality and uniqueness describe the position of an individual species' traits in a community's trait hyperspace. Specifically, trait originality measures the distance of a species' traits to the centroid of trait space given the other species present (i.e. how its traits differ from the community average; Pavoine et al. 2005; Laliberté and Legendre, 2010). In contrast, uniqueness measures the distance of a species to its nearest neighbour in trait space (i.e. how unique the traits of a species are within the community; Walker, 1995; Julliard et al. 2006). While conceptually similar, they represent opposing community dynamics; while two species can be simultaneously functionally original by having a combination of traits differing from that of the community average, they may not be unique if they are similar to each other in their trait combinations (Coux et al. 2016). Indeed, these metrics are complimentary to each other.

Trait originality and uniqueness thus indicate the average rarity of a species' biological features in a community Buisson et al. (2013). By proxy they are indicative of the level of functional niche partitioning occurring. High levels of originality or uniqueness within a community would suggest less overlap in inter-specific resource use and reduced direct resource competition, whereas low originality or uniqueness would indicate growing redundancy within functional niches and potentially greater interspecies resource competition (in which one would expect increases in trait uniqueness to arise).

To calculate trait originality and uniqueness I used the function by Coux, (2016), which uses the package 'FD' (Laliberté and Legendre, 2010; Laliberté and Shipley, 2014) to calculate trait space and metrics using those trait space coordinates provided by the function.These metrics were calculated for each trait data set at each sampling occasion and used as predictor variables in subsequent mixed-effects models.

5.1.2 Distance from trait optimum

Distance from trait optimum is a metric which aims to determine the level of deviation from environmentally selected trait optima (Muscarella and Uriarte, 2016). This metric measures the absolute distance between each trait of each species in the community and the community's weighted mean trait values (i.e. plot-level trait values weighted by species abundances). Community weighted means (CWM) of trait data are one of the most routine methods ecologists use to assess the trait composition of biological communities and are used to determine how environmental conditions influence species abundances and distributions, mediated by their functional traits. Supporting this approach, is a plethora of publications reporting how CWMs respond to environmental gradients, disturbance and invasions. Most recently, Muscarella and Uriarte, (2016) showed strong support for the notion that CWMs reflect locally optimal phenotypes selected by the environment, particularly when considering multivariate trait space. To date, I am not aware of any study specifically defining distance from this trait optimum and investigating the role of such community properties in changes of species abundance.

Calculation of Distance from trait optimum is straightforward. Using the modified CWM calculation method of Peres-Neto et al. (2017): 1) Calculate the CWM as the product of trait values weighted by standardised species abundances at each site (CWM_{Wn}), 2) calculate the trait values of each species, s, weighted by their standardised total global abundance (T_{Ws}), 3) for each species trait subtract T_{Ws} from CWM_{Wn} and remove the sign to give $\Delta\, CWM_{ij}$.. Where traits were categorical variables, I calculated and used the relative proportion of each value. These values were calculated for each trait data set at each sampling occasion and used as predictor variables in subsequent mixed-effects models.

5.2 Testing changes of abundance in response to functional metrics: Mixed-effects regression

I used mixed-effects models to characterise and test how changes in abundance of each species responded to the three metrics describing its traits in relation to the community. First I calculated the change in species abundance between two sampling occasions for each possible temporal resolution (i.e. time series: $t_1 \rightarrow t_2$, $t_2 \rightarrow t_3$, and $t_1 \rightarrow t_3$) as the relative difference (i.e. $\Delta\ Abundance = (Adbundance_{t2} - Adbundance_{t1})/mean(Adbundance_{t1}, Adbundance_{t2})$. For each trait data set, time series and metric, I fit and tested a series of models with sites and species as crossed random effects. In addition, I tested each model including each trait metric from the initial sampling occasion, t_n, in parallel with a model including each metric calculated using the data from the final sampling occasion t_{n+1}. As well as the interaction between a species intial abundance and the trait metric. I used this approach because I had no *a priori* knowledge of the time scale over which competitive interactions would take place. Therefore, I tested whether the change in each species' abundance during the ten years between each sample was explained by either its traits relative to those of the community at the beginning of the ten -year period (i.e. a long timescale of effect) or at the end (i.e. a shorter-term effect).

The collection of models were fit and tested using a model simplification procedure and the best models selected by minimising AIC values as follows. Where Δ *Abundance* is the change in species abundance between sampling occasions t_n and t_{n+1}, β_1 is species abundance at the initial sampling occasion, t_n, to account for the possibility that changes in the abundance of a species may depend on its initial abundance, β_2 is the trait metric at either the first (β_{2_n}) or final ($\beta_{2_{n+1}}$) sampling occasion, and U and W are the random effects of site

and species :

$$\begin{aligned}
\Delta\ Abundance &= \beta_0 + U + W + \epsilon \\
&= \beta_0 + \beta_1 + U + W + \epsilon \\
&= \beta_0 + \beta_{2_n} + U + W + \epsilon \\
&= \beta_0 + \beta_1 + \beta_{2^n} + \beta_1 \times\ \beta_{2^n} + U + W + \epsilon \\
&= \beta_0 + \beta_1 + \beta_{2^{n+1}} + \beta_1 \times\ \beta_{2^{n+1}} + U + W + \epsilon
\end{aligned}$$

All models were fit using the lmer function of the package lme4 (Bates et al. 2015). I confirmed these models met the assumption of normality by checking the residuals for a normal distribution and homoscedasticity. lmerTest (Kuznetsova et al. 2016) was used to provide P-values to assess the significance of fixed-effects (calculated from F statistics using Satterthwaite's approximation for denominator degrees of freedom) and AIC values to asses model fit. The above analysis used all traits from each category (reproductive or vegetative) when calculating the trait metrics. In addition, I also compared models using a combination of the metrics to assess their relationships with each other. Finally, modelling results are presented in tables which were constructed with assistance of the package 'texreg' (Leifeld, 2013).

Chapter 6

Results: Does change in abundance of species depend on uniqueness and originality (competition) or distance from the optimal community traits (environment)?

6.1 The effect of trait uniqueness on change in abundance

The ability of a) initial species abundance and trait uniqueness (the distance of a species in trait space to its nearest neighbour), b) final trait uniqueness, and c) the interactions of these terms, to explain changes in species abundance over time (Δ *Abundance*) changed across each sampling period (Table E.1 to Table E.3). This result was similar when the models were fitted in parallel with trait data partitioned to include vegetative or reproductive traits only (Table E.4 to Table E.6).

In the model of best fit for the first sampling period (1980's to 1990s), initial abundance (t_1) was an important predictor of changes in species abundance($p < 0.001$), after controlling for site and species level random effects (Table Table E.1, Model 3, $AIC = 6028.760$). High initial species abundances had a negative effect on ΔAbundance, that being species more abundant at the first sampling period were highly likely to have a larger decrease in abundance when measured at the second sampling period. Uniqueness never attained significance. The models of best fit for both the second sampling period ($t_2 \rightarrow t_3$; Table E.2, $AIC = 59252.414$) and the entire sampling period combined ($t_1 \rightarrow t_3$; Table E.3, $AIC = 6253.869$) included the same significant parameter of initial abundance. The strong negative effect of initial abundance on ΔAbundance remained significant, uniqueness was never significant.

A similar overall pattern of best fitting models was obtained when fitting the vegetative and reproductive trait data separately (Table E.4 to Table E.6). The models which included initial abundance, final uniqueness and the interaction term were always selected as the best fitting, as indicated by lowest AIC values. Likewise, the significance of parameters varied between sampling periods for both trait categories in similar patterns. The strength of the effect for parameters did differ between the trait datasets, however. For both trait data sets, initial abundance always showed a negative relationship with ΔAbundance ($p < 0.001$), indicating that more abundant species would undergo a larger reduction in abundance over time, as in the previous models. Vegetative trait final uniqueness also had a negative relationship with ΔAbundance. Thus, as species increased in abundance over time, the resulting community's vegetative traits would become more similar. This relationship remained significant for the $t_1 \rightarrow t_2$ and $t_1 \rightarrow t_3$ sampling periods ($p < 0.1$) and the $t_2 \rightarrow t_3$ ($p < 0.05$). The interaction between initial abundance and final uniqueness never attained significance for vegetative traits. In contrast, the final uniqueness of reproductive traits showed a positive relationship with ΔAbundance, however, this never attained significance. Across the sampling periods, the relasionship between ΔAbundance and ini-

tial abundance attained a similar pattern of significance to final vegetative trait uniqueness ($t_1 \rightarrow t_2,\ p < 0.01;\ t_2 \rightarrow t_3,\ p < 0.01;\ t_1 \rightarrow t_3,\ p < 0.01$). This would suggest that inter-specific competition has a much greater effect on change in species abundance over time, and uniqueness is strongly selected against.

6.2 Effect of trait originality on change in species abundance

The ability of a) initial species abundance and trait originality (abundance weighted and binary weighted species distance to the community centroid), b) final trait originality, and c) the interactions of these terms, to explain changes in species abundance over time changed across each sampling period (Table E.7 to Table E.9). Model fit, as indicated by lower AIC values, was consistently better for abundance weighted originality in contrast to binary (Presence/Absence) weighted originality. Therefore results including originality$^{P/A}$ are omitted from discussion but their tables are included in the appendix (Table E.7 to Table E.9). These results were similar when the models were fitted in parallel with trait data partitioned to include vegetative or reproductive traits only (Table E.10 to Table E.12).

Across all sampling periods, models including the parameters *initial abundance*, $final\ originality$ and *initial abundance* $\times$ $final\ originality$, gave best fits as indicated by the lowest AIC values. For the best fitting models across sampling periods all of the aforementioned parameters remained significant ($p < 0.01$; Model 3, Table E.7 to Table E.9) in the complete trait dataset with the exception of interaction term for the entire study period ($p < 0.1$; Model 3, Table E.7). Across all sampling periods Δ *Abundance* showed a relatively weak negative response to *initial abundance* and a relatively strong negative response to $final\ originality$. The effect when considering *initial abundance* $\times$ $final\ originality$ interaction was relatively small however, which is unsurprising as originality is an abundance-weighted measure of the average distance of a species to the community trait centroid. This suggests a similar pattern

to the uniqueness measures in community response: highly abundant species are likely to have a greater decrease in abundance over time, and as this occurs, species-trait syndromes converge on the community centroid (i.e. less variation in traits at the community level).

Models of best fit and patterns of significant parameters were similar when considering the vegetative and reproductive trait originality separately. As with previous measures model including *initial abundance*, $final\ originality$, and *initial abundance* $\times$ $final\ originality$ gave best fits as indicated by the lowest AIC values. Overall, the models showed similar results to those for the full trait dataset.

6.3 Effect of distance from community-trait optimum on change in species abundance

The fact that communities moved towards being dominated by species close to the trait centroid, as shown by the previous sections, suggests some traits in those communities are advantageous to have. I therefore expected that those traits at the centroid reflect the optimum traits for the given environment. The ability of a) initial species abundance and Δ $Community\ Trait\ Optimum$ (Δ CTO; the difference between a species traits and the community-weighted mean), and b) the interactions of these terms, to explain the changes in species abundance over time changed over time (Table E.13 – Table E.15), and remained so for both vegetative and reproductive traits when modelled separately (Table E.16–Table E.18).

The best fitting model for each data set was always model 3. This model included both ΔCTO and initial abundance, as well as the interaction term. The models for all three data sets (i.e. all traits, vegetative traits, reproductive traits) showed relatively consistent parameter inclusions and significance levels. For the first period ($t1 \rightarrow t2$, Table E.13), ΔCTO showed a negative effect ($p < 0.001$) , initial abundance has a positive effect ($p < 0.001$), and the interactive effect of these two parameters rounded to zero (likely slightly positive,

$p < 0.001$). This suggests that part of the negative effect of initial abundance is due to abundance being correlated with ΔCTO. For the second period ($t2 \rightarrow t3$, Table E.14), the effect of ΔCTO remained negative ($p < 0.01$), however this time initial abundance ($p < 0.01$) switched sign, showing negative effects. The model for the entire study period ($t1 \rightarrow t3$, Table E.15) was congruent with that for the first periods model, where ΔCTO was a negative effect ($p < 0.01$), initial abundance was a negative effect ($p < 0.01$), and the interaction term was very weak but positive ($p < 0.01$). This pattern of parameter significance and their effects were nearly identical when considering vegetative and reproductive traits separately (Table E.16 to Table E.18). In summary, the coefficients suggest more abundant species become less abundant over time, and that species which are poorly matched to their environment (i.e. a large distance from the optimum) decrease in abundance, or at least show less of an increase in abundance.

6.4 Effect of uniqueness and originality, combined with distance from community-trait optimum, on change in species abundance

In addition to the above models, I also fitted a series of additional ones to investigate the response of each metric to the inclusion of another in the model. The specific purpose of this was to investigate how the effect of each parameter changed when considered in the same model. When $\Delta\ CTO$ was included in a model with either uniqueness or originality, the effect of $\Delta\ CTO$ was non-significant (Table E.19—Table E.30) . This implies that uniqueness and originality are collinear with $\Delta\ CTO$. This means some of the variance for change in abundance due to being distant from the environmentally selected optimum could also be explained by being original or unique and inspection of diagnostic scatter plots, where values of each variable are plotted against each other, supported this . However, there appeared to

be a downward trend in all the residual vs. fitted plots, which suggests that the models over-predict large change in abundance and under-predict small ones. In all cases however, AIC values indicated that the model including initial abundance, originality and the interaction of these terms was the best fit for the data.

Chapter 7

Discussion

7.1 Summary

In this thesis I used two overarching research questions to investigate whether environmental selection for plant functional traits influences species' population trajectories, which bears relevance for both native species decline and spread of invasives. These two questions were: a) How do environmental drivers of change influence species and trait composition (and can these influences be detected over the influence of spatial processes)? and b) how does the trade-off between competitive release (associated with novel traits) and environmental filters on community traits determine the success of species? I addressed these questions by testing a number of hypotheses pertaining to each. In doing so, I did not find support for my hypothesis that it is advantageous for species to have a novel (unique or original) set of traits, and that this advantage would be reflected in novel species increasing in abundance over time. Instead, I found that the environment shaped species traits, and that species with traits that deviated from those determined by environmental filters decreased in abundance.

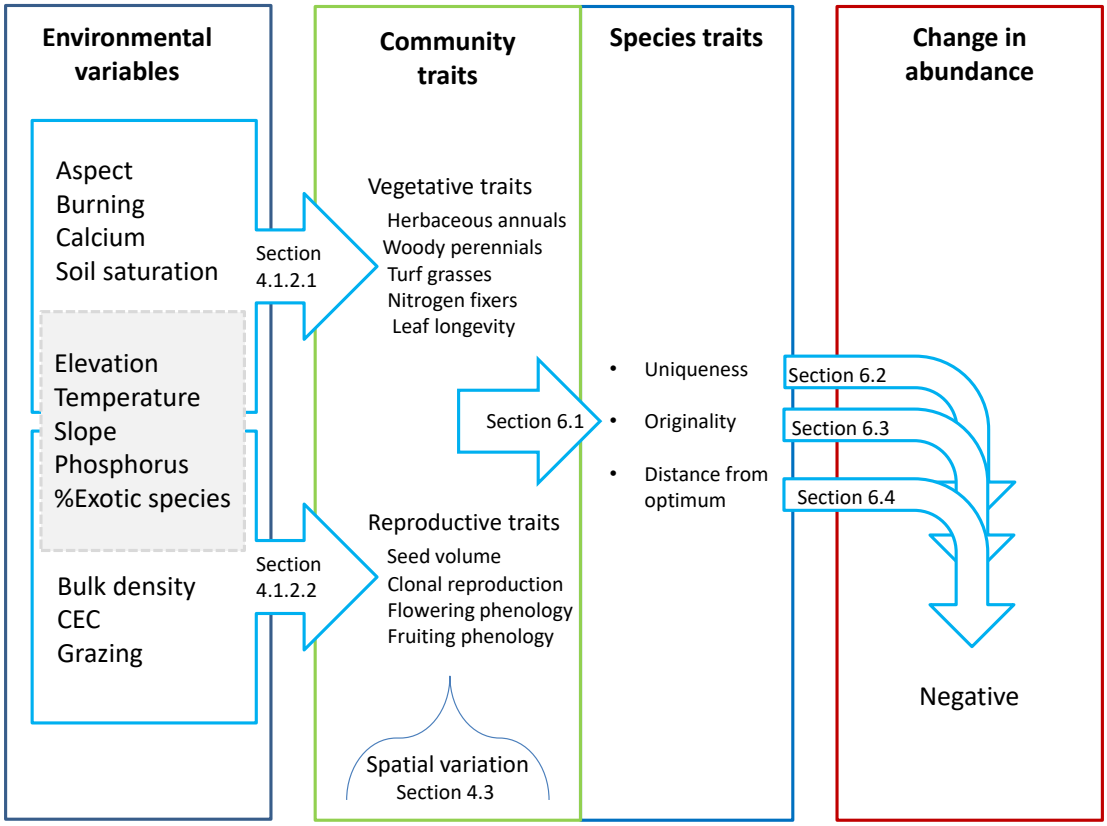


Figure 7.1: Pathways through which important environmental variables select for community-trait composition, which in turn acts to generate a change in species abundance. The dashed environmental variable box indicates variables which are important for both vegetative and reproductive traits. Relevant result sections for each pathway are given on the respective arrow.

7.2 How do environmental drivers influence community trait composition?

For the first question, I used the *RLQ* and Fourth-corner approach to characterise how the community composition of species and traits is influenced by measured environmental variables, and to test the hypothesis that traits and the environment are linked. I found strong support for rejecting the global null hypothesis, by testing a series of sub-hypotheses, which each individually addressed the three-way relationship between species, traits and the environment (Section 4.1). In all cases I showed that the composition of both vegetative and reproductive traits in a community depends on both local species composition

and environmental conditions (Section 4.1.1). Moreover, I highlighted the nature of general patterns in this three-way relationship and the specific response of individual traits to environmental variables. In addition to this, I used Moran's Eigenvector Maps (MEMs) to characterise whether these results differ, or remain similar, when analysed at multiple spatial scales. Again, I was able to reject the global null hypothesis at both the landscape scale (<120 km) and the regional scale (>120 km), while showing that the nature of trait—environment relationships varies between spatial scales (Section 4.3). I will discuss vegetative and reproductive traits separately below.

7.2.1 Environmental drivers of vegetative trait composition

Using RLQ and fourth corner analyses, I illustrated several dominant trait–environment relationships. These relationships were indicated for both categorical and continuous traits and environmental variables. Maximum height was the only continuous variable to show significance; surprisingly, this was positive with slope. I expected height and elevation (not slope) to show a strong negative relationship, as the tree line in the study area is typically around 800-1000m, although this was not the case. It is possible that elevation has an increasingly positive correlation with slope. However, environmental variable correlation plots for vegetative trait diversity (Figure 4.5b) showed that the influence of elevation on community trait composition was roughly orthogonal to slope, with slope being more similarly positioned on the axes to burning. In addition to (and correlated with) elevation, I would have also expected temperature to be a determinant of plant height. Mason et al. (2013a) showed that the maximum height of tree species occurring in NZ grasslands is generally determined by temperature, and indeed, temperature is also a key determinant of forest canopy height in New Zealand, where it markedly declines below a mean annual temperature of 9 °C (Mason et al. 2012). However, temperature was not significantly associated with height.

Given the analyses I have presented, which shows a strong positive relationship between height and slope, and no clear determination of the relationship between height and other life-

form traits (see Figure B.1), it is likely that locations of increased slope provide refuge from a combination of stressful abiotic and biotic conditions that would otherwise limit growth height, such as temperature and land-use patterns. Other recent studies of plant functional trait distributions in alpine ecosystems (i.e. Australia and China) have shown similar results, that tree height is positively associated with slope. They demonstrated that leaf area, xylem traits, and most importantly maximum tree height, were key determinants of tree positions on slopes that form natural cold air accumulation gradients (Lim et al. 2017). On lower positions along slopes, shorter species with smaller leaves, and lower vessel density (i.e. less woody) were more common. In addition, increased slope is likely to further reduce abiotic stress for woody species due to greater water availability through increased cloud water deposition (Campbell and Murray, 1990; Cameron et al. 1997), thereby benefiting woody species in contrast to grass species (Parolari et al. 2015). Moreover, the additional pattern of increased woodiness with decreased land-use intensity (i.e. ungrazed or conservation estate vs Pastoral grazed; Figure 4.1), matches previous results found in grasslands globally (Uhl et al. 1988; Fischer and Wipf, 2002; Cramer et al. 2008). I also found that woodiness was also associated with increased evidence of burning, potentially because burning reduces grass cover enough to allow woody species establishment and selects for species with traits that confer increased re-sprouting ability (Müller et al. 2007). Increased evidence of burning was also shown to be associated with increases in slope (Figure 4.5), and this is possibly because burning is an effective means to clear vegetation from topographically challenging areas. Therefore, these results suggest that historical land-use practises (such as burning) facilitated taller woody species establishment through reduction in resource competition (i.e. light and water). Following this, slope then provides topographical relief of some environmental filters (e.g. temperature and grazing intensity) enabling woody species persistence over the long term.

Nitrogen fixing and deciduous species also showed strong environmental associations, which were revealed using the fourth corner analysis (Table 4.1). Environmental variables

that indicate good pastoral sites (e.g. increased soil water content, calcium, phosphorus, temperature and decreased elevation) tended to drive the community away from evergreen species (e.g. *Veronica pulvinaris*, *Hectorella caespitosa*) and toward nitrogen fixing (e.g. *Lotus pedunculatus*, *Vicia sativa* , *Trifolium* sp.) and deciduous (e.g. *Rosa rubiginosa*) species. Communities featuring nitrogen fixing or deciduous species typically contained a high proportion of exotic species, which is to be expected as there are relatively few native nitrogen fixers or deciduous species in this data set. Most of the nitrogen fixers present, both native and exotic, are highly palatable species (e.g. *Carmachellia* sp., *Trifolium* sp.). Therefore, given that these patterns were observed at the regional scale (Figure D.1b), nitrogen fixing ability may indicate nearby pastoral-type land use, as increased abundances of these species likely stems from increased propagule pressure in the surrounding landscape (Mason et al. 2013a; Warren et al. 2013), which is in turn driven by historical or presently increasing agricultural intensification of the surrounding region. Supporting this expectation is the known pattern that nitrogen fixing species have a strong negative association with nitrogen deposition and a positive association with soil phosphorus content, which has been well discussed in the wider literature (e.g. Vitousek et al. 2002).

Increased soil nitrogen availability is likely to promote two synergistic positive abiotic and biotic feedbacks, which act to enhance grassland invasibility, promote native species decline, and impact long-term ecosystem functions such as carbon storage. First, increased soil nitrogen availability enables increased rates of growth in competitively superior exotic grass species (Tilman and Wedin, 1991) and supports the rapid and early seasonal growth of exotic deciduous species (Aerts, 1990). This in turn increases competitive pressure on native grassland herbaceous and woody species for resources such as water, light, and nutrients (Standish et al. 2008). Second, changes in species composition associated with the above competitive interactions are likely to promote a reduction in temporal scales of fire, through increased standing-mass and litter carbon stocks, which act to increase grassland flammability (Cheng et al. 2013; McGlone et al. 2014; Perry et al. 2014). Fire frequency

has been illustrated here (see Table 4.1), as well as in previous literature (McGlone et al. 2014; Perry et al. 2014), to have a strong negative effect on tussock species. Together in the long term, these above processes may act to create a feedback loop of fire disturbance and nitrogen loss (through fire volatilization; Evans et al. 2001), which enables re-invasion by nitrogen fixers and competitively dominant deciduous species, and thus resets the feedback loop (Evans et al. 2001; Brooks et al. 2004).

7.2.2 Environmental drivers of reproductive trait composition

In addition to the above trait–environment relationships, the RLQ and 4th corner analyses uncovered a small number of reproductive trait–environment relationships. Significant relationships were identified for seed volume, tiller production (i.e. clonal reproduction in grasses) and flowering and fruiting phenology. Seed volume was shown to have a positive relationship with slope, and was the only continuous reproductive trait to attain significance.

Seed volume plays important roles in dispersal, seedling establishment and survival (Poorter et al. 2008), as well as persistence in the seed bank (Thompson et al. 1993). Similarly, seed volume may be used to predict potential growth rates and canopy height, particularly under low-resource conditions (e.g. biotic and environmental filtering; Poorter et al. 2008). As seed size increases, it is expected that seeds will better persist in the seed bank (Thompson et al. 1993), new germinants will have greater initial resource reserves to successfully establish under negative carbon balances (e.g. low light and water conditions; Lieberman and Li, 1992; Lopez and Kursar, 2007; Myers and Kitajima, 2007), and thus increased chance of escaping size-dependent mortality (Paz et al. 2005) or to recover from damage due to herbivory or falling debris (Harms and Dalling, 1997). I hypothesise that there are two potential mechanisms underlying the tendency for increased size of seed with slope, and these depend on the initial vegetation state present. First, where seeds disperse to sloped areas that have no initial under-story vegetative cover (i.e. bare ground under shrubs), larger seeds will have a greater chance of resisting down-slope transportation (e.g.

by gravity or water; Sarneel, 2016) to unsuitable germination sites with lower temperatures, and increased seed bank persistence due to their larger size (Thompson et al. 1993). Second, above the tree line where grass cover is high, larger seeds would better facilitate the initial growth required to reach seedling size and escape the low-light conditions within the grass sward (Jakobsson and Eriksson, 2000). Various studies on the mechanics of woody species encroachment of grasslands support both of these general hypotheses (Jakobsson and Eriksson, 2000; Jensen and Gutekunst, 2003; Moles and Westoby, 2004; Kalamees and Zobel, 2002; Hopfensperger, 2007).

The positive relationship between species possessing tillers and reduced grazing intensity is unsurprising. Tillers are associated with grass species that tend to respond negatively to frequent grazing (McGlone et al. 2014). Tillers provide a means for the clonal reproduction and recruitment of grasses, thus facilitating 'site filling' and canopy expansion (Lord, 1993; Lemaire et al. 2000). While a level of grazing is important to maintain native species dominance in highly invaded short-tussock grasslands (Lord, 1990; Rose and Platt, 1992; Rose and Frampton, 2007; Duncan et al. 2001; Day and Buckley, 2011), it has been shown that the mechanisms by which once widespread native avifauna browse (e.g. takahe *Notornis mantelli*) removed less tiller biomass than more indiscriminate introduced-undulate browsing (Mills et al. 1989); a pattern which is reflected globally (Parker et al. 2006). Thus my analysis highlighting the positive association between tiller presence and reduced browsing intensity reflects this.

Several flowering and fruiting phenologies were associated with environmental variables. These associations were both positive and negative relationships, and appeared to follow a similar land-use type gradient as shown for vegetative traits in Figure 4.2; that being, a general gradient from environmental conditions which indicate suitable agricultural sites, through to sites which would be less suitable to agricultural use. Flowering ending in winter was positively associated with pH, soil phosphorus content and soil bulk density, while negatively associated with soil cation exchange capability and elevation. Conversely, fruiting

beginning in spring was positively associated with temperature, and negatively with elevation. The environmental variables showing positive associations for these flowering and fruiting traits were significantly associated with pastoral land use, whereas the negative trait-environmental associations were associated with variables indicating lower grazing intensity (i.e. grazing removed or not grazed, see Figure 4.2).

The flowering and fruiting phenologies observed are therefore likely to be a product of agricultural selection. Specifically, the land-use types and changes occurring in this study area may be selecting for new syndromes of life-history traits. For example, winter flowering could be advantageous to avoid grazing pressure on reproductive organs, with the cost that these organs need to be tolerable of frost damage. It would also mean that seed set and dispersed would need to withstand lower temperatures, with the benefit of reduced invertabrate seed predation and being able to get ahead of other species when seed germinates in spring (Sanchez et al. 2012). I am not aware of any literature that shows the ecological consequences of this in the context of invasion. However, these life-history strategies are typically associated with both desirable and undesirable, annual and biennial species (Diaz et al. 2007). Therefore, they likely represent a trajectory of invasion more similar to that of abandoned pastures (Peco et al. 2005; Peco et al. 2012; Cramer et al. 2008), rather than a shift in composition to perennial grassland species.

7.3 Does past community trait composition influence future trait composition?

The above discussion emphasises the influence of the environment on community vegetative and reproductive traits. However, in addition to these environmental filters, community and trait composition can be influenced by interactions among community members (Macdougall and turkington, 2004; MacDougall and Turkington, 2006; Kunstler et al. 2012; Luzuriaga et al. 2012). I initially hypothesised that species that avoid competition with others, by having

novel traits, will receive fitness benefits, and thus that they should increase in abundance. This hypothesis, which places emphasis on species interactions, rather than the environment as filters, was not well supported by my results. Instead, I found that the environment shaped species traits, and that species with traits that deviated from those determined by environmental filters decreased in abundance, even if this deviation from the environmentally optimal traits was also associated with having novel traits relative to the community (see Chapter 6).

The above outcome was determined by examining the direction and strength of relationships between changes in species abundance between sampling occasions, competitive release (associated with novel traits) and environmental filters on community traits. Overall, I largely found that the distance from the environmentally selected community trait optimum ($\Delta\ CTO$) exerted the strongest effect on the trajectory of species abundances (in Section 6.4), and that this measure tended to explain variance in species abundances that was also associated with trait novelty. Additionally, initial species abundance, originality (distance to the trait centroid) and uniqueness (distance to the nearest neighbour) of traits, all negatively affected the change in a species' abundance over time. However, the negative effect of originality and uniqueness was often weakened or eliminated when the distance to the environmentally selected traits was also included in the model (see Table E.20 & Table E.25). This suggests that both measures of trait novelty were collinear with $\Delta\ CTO$, such that having novel traits tended to come at a cost of being further from the environmental optimum.

In all cases, high initial abundance resulted in larger declines of abundance over time (e.g. Table E.12). This pattern may be a result of strengthening intra-specifc competition, changes in optimal environmental conditions over time, or natural fluctuations in species population sizes, which are all common processes during the stages of invasion (Courchamp et al. 1999; Groom, 1998; Taylor and Hastings, 2005; Tobin et al. 2007). However, having high initial abundances tended to reduce the strength of the negative effect of possessing novel traits or

being a poor match to the environment (see Table E.15). This interaction suggests that a density dependent process, be that trait—environment or biotic interactions, buffered large changes in abundance, that would occur due to being novel or a poor environmental fit. Interestingly, uniqueness appeared to have dissimilar main effects when comparing vegetative and reproductive traits separately; whereas uniqueness for vegetative traits always had a significant negative effect on species trajectory, uniqueness of reproductive traits had a positive trend (see Table E.5). However, this relationship was always non-significant, except for one case in which distance from the environmentally selected optimum was included in the model. During the period between the 1980's and 1990's sampling occasions, moving into a unique trait space had a weak, but significant, positive effect ($p < 0.05$, Table E.22). This pattern occurs during a period where the diversity of native small-herb species substantially declined, while woody species remained constant and *Chionochloa* and *Heiracium* species abundances increased (Duncan et al. 2001). Following this, species diversity appeared to recover (Day and Buckley, 2011; Day and Buckley, 2013). It would therefore be interesting to test the mechanisms that underpin this pattern, though this result should also be treated with caution as a significant effect during only one sampling period could occur through type I error.

Community assembly theory suggests that dispersal, abiotic, and biotic filters act in a heirachical structure during community assembly (Luzuriaga et al. 2012). This model suggests that given successful dispersal to a site, a species' ability to persist and reproduce will first depend on its ability to withstand the abiotic conditions present, then on the species' ability to coexist given the other species present in the community. The results I present here suggest that, for this grassland system, the relative importance of environmental constraints on a species' population trajectory, which are mediated by the species' traits, is stronger than that of inter-specific competitive interactions. This result is supported by an array of studies across multiple ecological systems (Funk and Vitousek, 2007; HilleRisLambers et al. 2012; Lebrija-Trejos et al. 2010). However, legacy effects (i.e. time-lagged effects of previous

environmental modifications, Bürgi et al. (2017); see also Section 1.2) and disturbance regimes also have an important role in understanding population trajectories (Funk et al. 2008), particularly when considering dispersal filters (Mason et al. 2013a), as well as when placed in the context of invasions (Maoela et al. 2016; Hobbs et al. 2009).

In addition to theory pertaining to filters on community assembly, community ecology theory predicts that invasive species will be unlikely to establish or persist if there is a species with similar traits present in the community or if available niches are filled (i.e. limiting similarity; Funk et al. 2008). This prediction aligns with my original, yet unsupported, hypothesis that novel traits would be advantageous to species. As the data for this study were collected long after widespread modification of this system (Duncan et al. 2001), we are only able to hypothesise on the original species and trait compositions. This highlights limitations as to why I may not have found support for this prediction. Firstly, there is no reference against which to accurately determine the unmodified-grassland trait composition (see Section 1.2). We are therefore unable to determine the extent to which recent exotic invaders posses novel traits in comparison to the traits in the original community. Second, evidence exists that disturbance is primary driver of novel traits across multiple ecosystem types (Mouillot et al. 2013; Brandl et al. 2016) . Furthermore, invaders that are 'ecosystem engineers' may modify the environment to the effect that the composition of environmentally selected optimum trait shifts, thus modifying other species' population trajectories. Therefore, I finally propose that for novel traits to enable increases in species abundances, a disturbance first needs to perturb the system in a manner which creates vacant niches to invade (e.g. removal of canopy or extinction of species), and for these novel traits to facilitate long-term increases in abundance they need to match both current and future environmental constraints.

7.4 Study limitations

There are a number of limitations that need to be considered when drawing conclusions from the results of my thesis. These limitations largely pertain to the sources and subsequent use of the data. First, as discussed in Section 2.1, while representative of the study area, the study sites from which species abundance data were collected were not randomly sampled. The original data collection was carried out with the intent of being used to observe changes in species diversity due to varying land-use types and management regimes (Duncan et al. 2001), and as a result some sites were spatially clustered. In order to address this issue, in my first data chapters I carried out spatial analyses (Moran's Eigenvector Maps) to test and account for the spatial structuring of both species and environmental data. This exercise successfully identified trait—environment relationships that occurred at multiple spatial scales, although the significance of some relationships at the 'global' scale was lost.

The second chapter, which utilised a mixed-effect modelling framework, I accounted for spatial dependence by including a site level random effect. The second major limitation is that the trait data was complied from various databases and is based on mean trait values for each species. Therefore, the quality of the trait data is only as robust as the location from which it was sourced. Additionally, as the trait data represent mean population values, it ignores potential intra-specific variation of traits. This means that I am unable to draw conclusions upon the influence of environmentally-induced phenotypic variation, which has shown to play an import role in plant invasions (Kichenin et al. 2013; Siefert et al. 2015; Crutsinger et al. 2009).

7.5 Conclusion

In conclusion, I have highlighted a potential disturbance-related feedback loop, whereby an increase of leguminous species associated with pastoralism may promote a reduction in the long-term frequency of natural fires. Additionally, I have also shown that environmental

selection for plant traits exerts a dominant force on the trajectory of species abundances, and that possessing novel traits to escape competition may come at a cost of being a poor fit to the environment. These two ecosystem process will require intense observation and management if we wish to prevent further long-term ecological decline of New Zealands' high-country grasslands. The reason for this is two-fold. First, under the currently widespread combined trends of increasing land-use intensification in lower elevations, the retirement of marginal land in mid-elevations, and projected climate change, plant species which promote the described fire-disturbance feedback loop are more likely to encroach into less modified higher elevations. Second, those tasked with restoring grassland ecosystems will be required to take into account the tradeoffs between environmental and biotic filtering of traits when selecting species to include in these novel communities, as well as their spatial configuration in the landscape. Doing so will assist in ensuring the success of, and reduce potential for conflict associated with, balancing economic activities and those that conserve and further enhance ecosystem functions. Moreover, my findings suggest that searching for traits of 'invasiveness', or even comparing invader traits to those of the community, may have limited value in predicting the success of invaders unless these are considered within the context of environmental trait selection. As global environmental changes exert new or modified environmental filters on species, they will alter population trajectories of species, and constrain their ability to escape competitive interactions by possessing novel traits. Jointly, these processes will determine the survival of species and the susceptibility of ecosystems to invasion.

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Appendices

Appendix A

Table A.1: List of vegetative and reproductive traits, and their descriptions, used in the analyses in this study. Each trait value represents a maximum mean or population-level value. Trait values were obtained from the online database of Landscare Research (http://ecotraits.landcareresearch.co.nz/), the New Zealand Plant Conservation Network (http://www.nzpcn.org.nz/) and several book resources (Allan et al. 1961; Stuppy, 2003; James et al. 2012). Examples of uses for each trait, their measurement and the theory underpinning their use is reviewed in Cornelissen et al. 2003 and Perez-Harguindeguy et al. 2013.

Trait	Type	Value &/or Units	Description
Vegetative traits			
Life mode	Categorical	Herbaceous annual; Herbaceous biennial; Herbaceous perennial; Ferns; Parasites; Woody perennial	Describes the life strategy of plants. Indicates resource use syndrome and ecosystem function
Growth mode	Categorical	Graminiform-Grasslike Sedge; Graminiform-turf Grass;Graminiform-tufted Grass; Junciform; Mat-Forming Dicot; Rosette Dicot; Semi-Rosette Dicot; Non-Rosette Dicot; Emergent Dicots; Climbing Dicot; Other Petalous Monocot; Shrub; Subshrub; Prostrate Shrub; Spreading to erect small shrubs; Tree	Describes growth strategy. Indicates resource use syndromes, responses to environmental conditions and effects on ecosystem function.
Height	Continuous	Meters	Max mean heigh of species
Leaf form	Categorical	Broad leaved; Grass leaved	Describes overall leaf form. Indicates resource use syndromes, responses to environmental conditions and effects on ecosystem function

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Trait	Type	Value &/or Units	Description
Leaf length	Continuous	Centimetres	Maximum mean leaf length; Indicates resource use syndromes and responses to environmental conditions
Leaf width	Continuous	Centimetres	Maximum mean leaf width; Indicates resource use syndromes and responses to environmental conditions
Leaf area	Continuous	Centimetres	Leaf length × Leaf width; Indicates resource use syndromes, responses to environmental conditions and herbivory
Shade tolerance	Categorical	Low; Intermediate; High	Indicates tolerance of stressful abiotic conditions (exposure) and competition
Spinescence	Binomial	Yes; No	Indicates resistance to herbivoury
Nitrogen fixation	Binomial	Yes; No	Indicates the presence of nitrogen fixing mutualisms and effects on ecosystem functioning
Leaf longevity	Categorical	Evergreen; Deciduous; Semi-evergreen	Indicates resource use and competitive ability
Reproductive traits			

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Table A.1 – continued from previous page

Trait	Type	Value &/or Units	Description
Seeds per plant	Categorical	0-10; 10-100; 100-1,000; 1,000-10,000; $>$ 10,000	Indicates potential seed production and reproductive output
Pollen vector	Categorical	Birds; Insect; Wind; Other	Indicates pollen transfer mode
Seed length	Continuous	Millimeters	Contributes to dispersal potential
Seed breadth	Continuous	Millimeters	Contributes to dispersal potential
Seed volume	Continuous	Millimeters	Seed length $\times$ seed breadth. Indicates to recruitment and dispersal potential
Above ground dispersal organs	Categorical	Creeping stems; Root suckers; Stolons; Tillers; None	Contributes to local dispersal potential, disturbance response, regenerative and competitive ability
Below ground dispersal organs	Categorical	Rhizomes; Tubers; None	Contributes to local dispersal potential, disturbance response, regenerative and competitive ability
Passive sexual dispersal mode	Categorical	Wind; Water; Unspecialised	Contributes to dispersal potential and competitive ability
Active sexual dispersal mode	Categorical	Ballistic; Endozoochory; Epizoochory; None	Indicates requirements for dispersal mutualisms

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Trait	Type	Value &/or Units	Description
Flowering Begins	Categorical	Spring; Summer; Autumn; Winter	Flowering phenology; Competitive ability and resource use
Flowering Ends	Categorical	Spring; Summer; Autumn; Winter	Flowering phenology; Competitive ability and resource use
Fruiting Ends	Categorical	Spring; Summer; Autumn; Winter	Flowering phenology; Competitive ability and resource use
Fruiting Ends	Categorical	Spring; Summer; Autumn; Winter	Fruiting phenology; Competitive ability and resource use

Appendix B

Table B.1: Vegetative trait *RLQ* analysis summary statistics showing the comparison of the inertia resulting from (a) the *RLQ* analysis (*RLQ*: three table ordination) which maximises the covariance between traits and the environment mediated by species abundance, and (b) co-inertia analyses ($R-L$ and $Q-L$: two table ordination), the individual parts of the *RLQ* analysis which maximise independently the traits (Hill-Smith analysis of trait variables), the structure of the environment (Hill-Smith analysis of environmental variables) and the correlation (correspondence analysis of sites-species table). The first two axis of the analyses are considered. Adapted from ...

(a) *RLQ*

Total inertia (λ):	2.36				
	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
Eigenvalues (λ):	1.88	0.220	0.131	0.036	0.025
Projected inertia (%):	79.93	9.31	5.51	1.53	1.08

	λ *decomposition*				
	λ	$Cov(Q,R)^2$	σ_R	σ_Q	$Cor(Q,R)$
Axis 1:	1.886	1.373	2.544	1.309	0.4123
Axis 2:	0.220	0.469	1.555	1.385	0.218

(b) *Inertia & co inertia*

	Inertia (λ)		Max (λ)		Ratio	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
R/R-L:	6.472	8.890	6.605	10.016	0.980	0.888
Q/Q-L:	1.714	3.631	2.793	5.270	0.614	0.689

	Correlation		Max		Ratio	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
L:	0.412	0.218	0.805	0.713	0.512	0.305

Inertia/Eigenvalues/λ, expresses projected variability; σ, the variance of the set of scores computed for one axis; Cov, the covariance of the two sets of scores projected onto the first and second *RLQ* axes. These values correspond to the latent roots of the analysis; $Cor(x,y)$, the correlation between the two sets of scores for each axis resulting from the *RLQ* analysis; Ratio, the amount of variance preserved between the *RLQ* analysis (Inertia) and the inertia (Max) from the Hill-Smith analysis or correlation from correspondence analyses.

Table B.2: Reproductive trait *RLQ* analysis summary statistics showing the comparison of the inertia resulting from (a) the *RLQ* analysis (*RLQ*: three table ordination) which maximises the covariance between traits and the environment mediated by species abundance, and (b) co-inertia analyses ($R-L$ and $Q-L$: two table ordination), the individual parts of the *RLQ* analysis which maximise independently the traits (Hill-Smith analysis of trait variables), the structure of the environment (Hill-Smith analysis of environmental variables) and the correlation (correspondence analysis of sites-species table). The first two axis of the analyses are considered. Adapted from ...

(a) *RLQ*

Total inertia (λ): 2.565

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
Eigenvalues (λ):	2.095	0.211	0.115	0.038	0.032
Projected inertia (%):	81.70	8.24	4.50	1.50	1.24

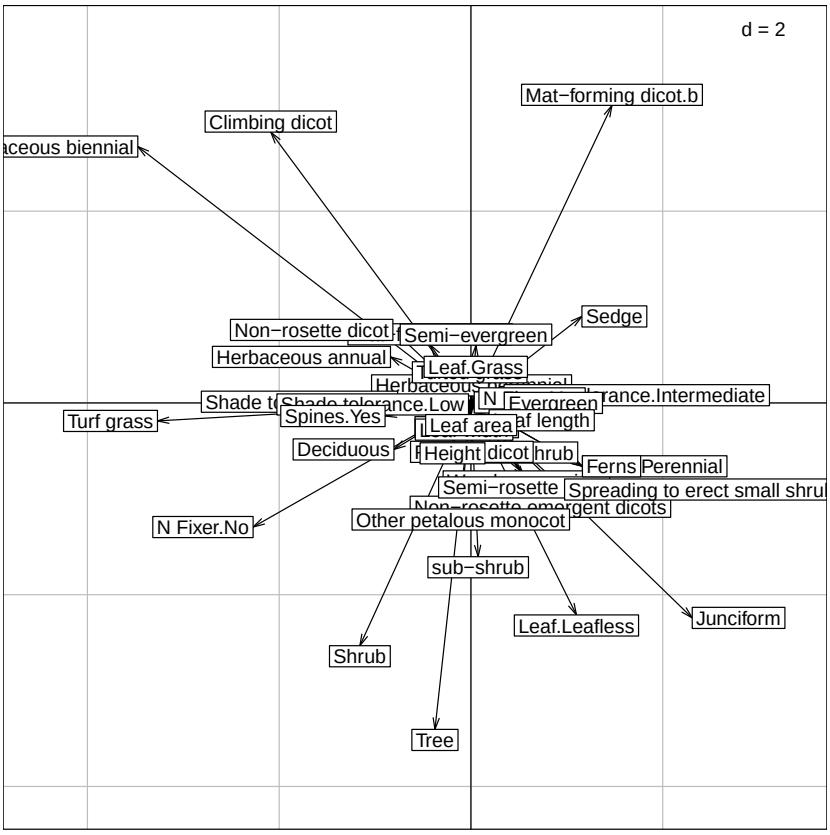
	λ *decomposition*				
	λ	$Cov(Q,R)^2$	σ_R	σ_Q	$Cor(Q,R)$
Axis 1:	2.095	1.447	2.550	1.615	0.351
Axis 2:	0.211	0.459	1.659	1.483	0.187

(b) *Inertia & co inertia*

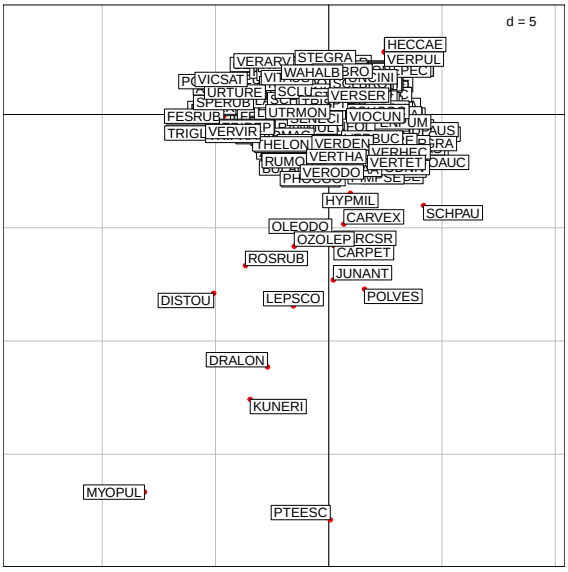
	Inertia (λ)		Max (λ)		Ratio	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
R/R-L:	6.507	9.261	6.605	10.016	0.985	0.925
Q/Q-L:	2.607	4.807	5.257	8.558	0.460	0.562

	Correlation		Max		Ratio	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
L:	0.351	0.190	0.805	0.713	0.436	0.262

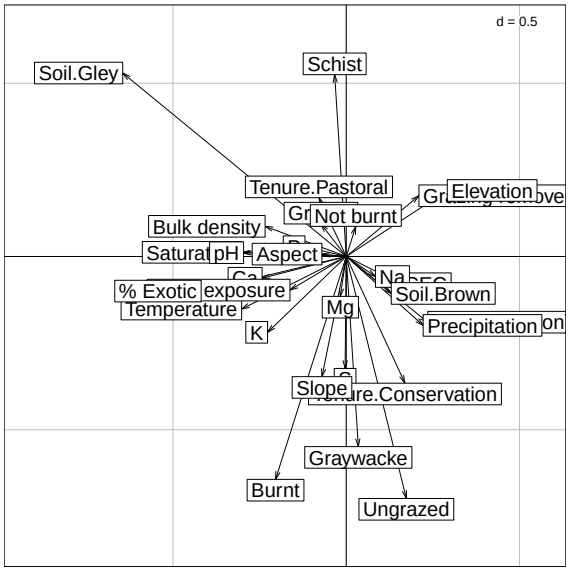
Inertia/Eigenvalues/λ, expresses projected variability; σ, the variance of the set of scores computed for one axis; Cov, the covariance of the two sets of scores projected onto the first and second *RLQ* axes. These values correspond to the latent roots of the analysis; $Cor(x,y)$, the correlation between the two sets of scores for each axis resulting from the *RLQ* analysis; Ratio, the amount of variance preserved between the *RLQ* analysis (Inertia) and the inertia (Max) from the Hill-Smith analysis or correlation from correspondence analyses.



(a) Trait scores

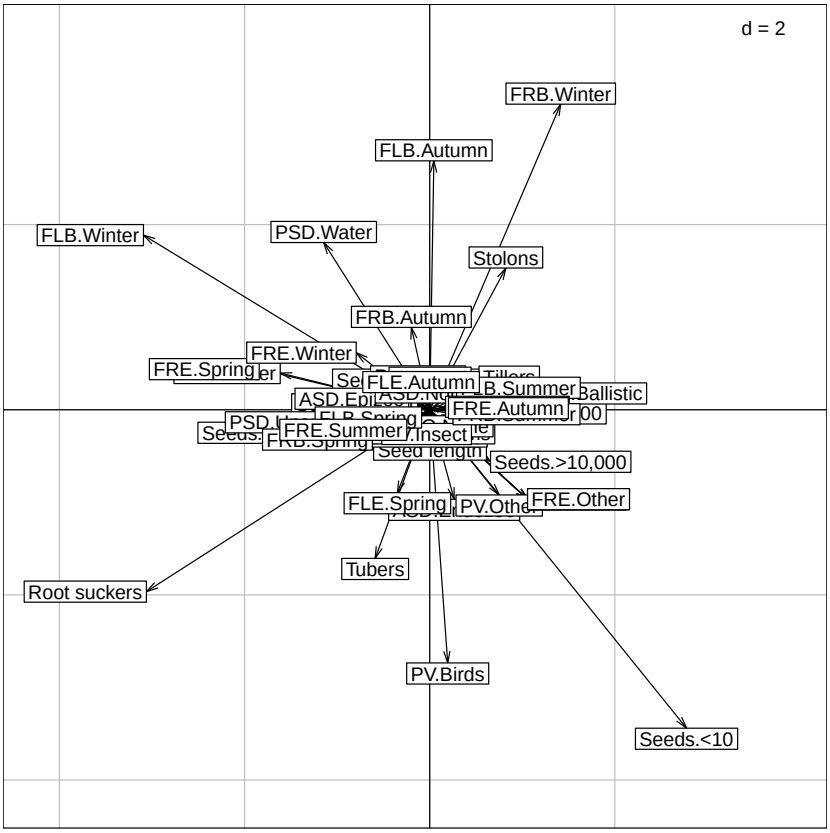


(b) Species scores

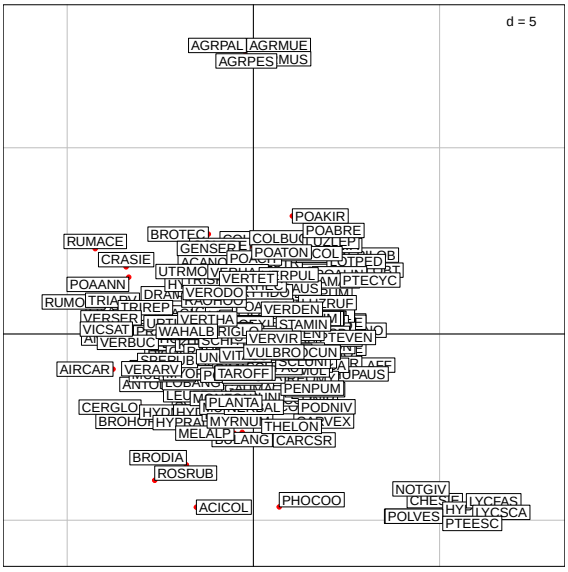


(c) Environment scores

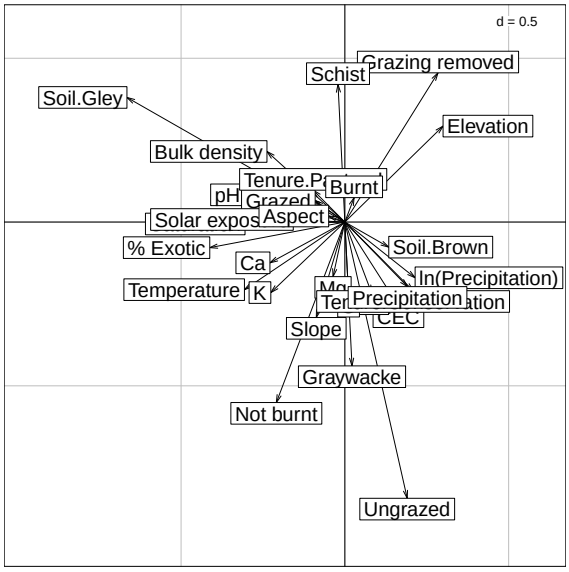
Figure B.1: Vegetative trait *RLQ* biplots showing (a) trait, (b) species and (c) environmental variable scores of the first two axes. Species codes are provided in Appendix E.



(a) Trait scores

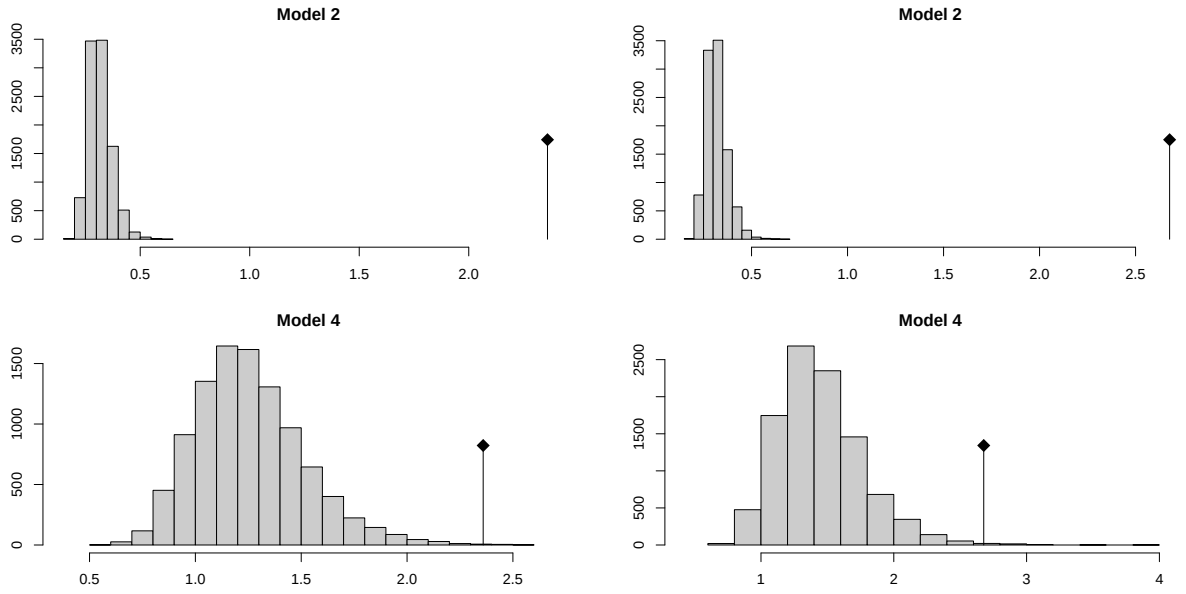


(b) Species scores



(c) Environment scores

Figure B.2: Reproductive trait *RLQ* biplots showing (a) trait, (b) species and (c) environmental variable scores of the first two axes. AGCO = Above ground clonal dispersal organ, BGCO = Below ground clonal dispersal organ, PSD = Passive seed dispersal, ASD = Active seed dispersa, PV = Pollen vector, FLB = Flowering begins, FLE = Flowering ends, FRB = Fruiting begins, FRE = Fruting ends. Species codes are provided in Appendix E.



(a) Vegetative traits **(b) Reproductive traits**

Figure B.3: Results of the multivariate procedure used to evaluate the significance of (a) vegetative and (b) reproductive trait-environment relationships. Bars show permuted expected interia values while the pin shows the observed inertia value. Model 2 permutes rows of the species table (sites), while Model 4 permutes columns of the species table. Both tests are highly significant for vegetative traits ($p = 0$ & $p = 0.001$) and reproductive traits ($p = 0$ & $p = 0.003$).

Appendix C

Table C.1: Results of the model selection procedure for the data driven computation of a distance threshold to be used in defining strength of connectivity between sampling sites. Model selection was carried out for each community composition data set. Ten distances were evaluated at regular intervals between the distance that maintained at least one connection to all sites (155.4 km) and the maximum distance between two sites (373.408 km).

Data	Species		Vegetative traits		Reproductive traits	
	D_{km}	$AICc$	D_{km}	$AICc$	D_{km}	$AICc$
	155.4	−71.84	155.4	−130.006	155.4	−111.811
	179.623	−72.768	179.623	−126.801	179.623	−110.41
	203.846	−72.774	203.846	−126.61	203.846	−110.765
	228.069	−71.331	228.069	−121.027	228.069	−111.183
	252.292	−72.871	252.292	−124.855	252.292	−112.353
	276.516	−73.033	276.516	−126.323	276.516	−115.361
	300.739	−74.658	300.739	−126.515	300.739	−111.07
	324.962	−76.471	324.962	−125.127	324.962	−116.894
	349.185	−75.356	349.185	−128.238	349.185	−114.181
	373.408	−73.7	373.408	−125.134	373.408	−113.753

Note: Shading indicates the model of best fit as indicated by the lowest $AICc$ values.

Table C.2: Results of the model selection procedure for the data driven computation of a distance distance decay power function for the Moran's Eigenvector Map spatial weighting matrix. The decay function was defined as $1 - (D/\Delta D)^y$, where $y = 2 : 10$. Model selection was carried out for the neighbourhood networks of each community composition data set.

Data	Species				Vegetative traits				Reproductive traits			
	y	D	$AICc$	$Nb.Vars$	y	D	$AICc$	$Nb.Vars$	y	D	$AICc$	$Nb.Vars$
	2	324.953	−68.767	4	2	155.4	−117.669	19	2	324.953	−102.409	7
	3	...	−76.471	9	3	...	−130.006	19	3	...	−116.894	18
	4	...	−72.597	5	4	...	−118.682	15	4	...	−105.77	7
	5	...	−72.148	5	5	...	−123.628	16	5	...	−112.392	12
	6	...	−71.574	5	6	...	−116.968	12	6	...	−106.91	11
	7	...	−71.714	5	7	...	−116.008	11	7	...	−109.923	12
	8	...	−71.44	6	8	...	−117.678	13	8	...	−110.189	10
	9	...	−70.792	4	9	...	−119.706	16	9	...	−107.303	11
	10	...	−71.184	2	10	...	−117.613	13	10	...	−106.457	10

Note: Shading indicates the model of best fit as indicated by the lowest $AICc$ values.

Table C.3: Summary statistics for the first two axes of the initial principle component analysis (PCA), redunancy analysis with environmental explainatory variables (RDA) and partitial-redundancy analysis with environmental co-variables (PRA) of species and trait composition. Varience is expressed in terms of inertia, where projected inertia is analogous to variance explained.

Data/Analysis	Total inertia	Eigenvalues	Projected inertia (%)	Cumulative inertia(%)
(a) Species				
PCA:	0.594			
Axis 1:		0.094	15.768	15.768
Axis 2:		0.079	13.304	29.072
RDA:	0.251			
Axis 1:		0.082	32.652	32.652
Axis 2:		0.043	17.099	49.751
PRA:	0.343			
Axis 1:		0.047	13.797	13.797
Axis 2:		0.025	7.27	21.067
(b) Vegetative traits				
PCA:	0.437			
Axis 1:		0.149	34.04	34.04
Axis 2:		0.106	24.22	58.261
RDA:	0.231			
Axis 1:		0.108	46.663	46.663
Axis 2:		0.063	27.43	74.093
PRA:	0.206			
Axis 1:		0.079	38.531	38.531
Axis 2:		0.026	12.488	51.019
(c) Reproductive traits				
PCA:	0.454			
Axis 1:		0.145	31.964	31.964
Axis 2:		0.107	23.542	55.506
RDA:	0.227			
Axis 1:		0.113	49.589	49.589
Axis 2:		0.055	24.417	74.006
PRA:	0.227			
Axis 1:		0.06	26.299	26.299
Axis 2:		0.04	17.526	43.824

Appendix D

Table D.1: Vegetative trait landscape-scale *RLQ* analysis summary statistics showing the comparison of the inertia resulting from (a) the *RLQ* analysis (*RLQ*: three table ordination) which maximises the covariance between traits and the environment mediated by species abundance, and (b) co-inertia analyses ($R-L$ and $Q-L$: two table ordination), the individual parts of the *RLQ* analysis which maximise independently the traits (Hill-Smith analysis of trait variables), the structure of the environment (Hill-Smith analysis of environmental variables) and the correlation (correspondence analysis of sites-species table). The first two axis of the analyses are considered. Adapted from ...

(a) Landscape-scale RLQ

Total inertia (λ): 0.6297

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
Eigenvalues (λ):	0.503	0.044	0.029	0.024	0.011
Projected inertia (%):	79.87	6.94	4.59	3.83	1.715

	λ decomposition				
	λ	$Cov(Q,R)^2$	σ_R	σ_Q	$Cor(Q,R)$
Axis 1:	0.503	0.709	2.641	1.230	2.185
Axis 2:	0.044	0.209	1.768	1.241	0.095

(b) Landscape-scale inertia & co-inertia

	Inertia (λ)		Max (λ)		Ratio	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
R/R-L:	6.971	10.096	7.013	10.953	0.994	0.991
Q/Q-L:	1.513	3.052	2.794	5.270	0.541	0.580

	Correlation		Max		Ratio	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
L:	0.219	0.096	0.806	0.714	0.272	0.134

Inertia/Eigenvalues/λ, expresses projected variability; σ, the variance of the set of scores computed for one axis; Cov, the covariance of the two sets of scores projected onto the first and second *RLQ* axes. These values correspond to the latent roots of the analysis; $Cor(x,y)$, the correlation between the two sets of scores for each axis resulting from the *RLQ* analysis; Ratio, the amount of variance preserved between the *RLQ* analysis (Inertia) and the inertia (Max) from the Hill-Smith analysis or correlation from correspondence analyses.

Table D.2: Vegetative trait regional-scale *RLQ* analysis summary statistics showing the comparison of the inertia resulting from (a) the *RLQ* analysis (*RLQ*: three table ordination) which maximises the covariance between traits and the environment mediated by species abundance, and (b) co-inertia analyses ($R - L$ and $Q - L$: two table ordination), the individual parts of the *RLQ* analysis which maximise independently the traits (Hill-Smith analysis of trait variables), the structure of the environment (Hill-Smith analysis of environmental variables) and the correlation (correspondence analysis of sites-species table). The first two axis of the analyses are considered. Adapted from ...

(a) Regional-scale RLQ

Total inertia (λ): 1.5

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
Eigenvalues (λ):	1.172	0.255	0.036	0.016	0.010
Projected inertia (%):	78.19	17.03	2.40	1.05	0.67
	λ *decomposition*				
	λ	$Cov(Q,R)^2$	σ_R	σ_Q	$Cor(Q,R)$
Axis 1:	1.172	0.083	2.689	1.338	0.301
Axis 2:	0.256	0.504	1.973	1.358	0.189

(b) Regional-scale inertia & co-inertia

	Inertia (λ)		Max (λ)		Ratio	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
R/R-L:	7.232	11.122	7.563	11.998	0.957	0.927
Q/Q-L:	1.791	3.636	2.794	5.270	0.641	0.690

	Correlation		Max		Ratio	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
L:	0.31	0.189	0.806	0.713	0.374	0.265

Inertia/Eigenvalues/λ, expresses projected variability; σ, the variance of the set of scores computed for one axis; Cov, the covariance of the two sets of scores projected onto the first and second *RLQ* axes. These values correspond to the latent roots of the analysis; $Cor(x, y)$, the correlation between the two sets of scores for each axis resulting from the *RLQ* analysis; Ratio, the amount of variance preserved between the *RLQ* analysis (Inertia) and the inertia (Max) from the Hill-Smith analysis or correlation from correspondence analyses.

Table D.3: Reproductive trait landscape-scale *RLQ* analysis summary statistics showing the comparison of the inertia resulting from (a) the *RLQ* analysis (*RLQ*: three table ordination) which maximises the covariance between traits and the environment mediated by species abundance, and (b) co-inertia analyses ($R - L$ and $Q - L$: two table ordination), the individual parts of the *RLQ* analysis which maximise independently the traits (Hill-Smith analysis of trait variables), the structure of the environment (Hill-Smith analysis of environmental variables) and the correlation (correspondence analysis of sites-species table). The first two axis of the analyses are considered. Adapted from ...

(a) Landscape-scale RLQ

Total inertia (λ): 0.3889

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
Eigenvalues (λ):	0.331	0.023	0.020	0.008	0.008
Projected inertia (%):	85.01	5.83	5.03	2.03	1.87
			λ *decomposition*		
	λ	$Cov(Q,R)^2$	σ_R	σ_Q	$Cor(Q,R)$
Axis 1:	0.331	0.575	2.145	1.531	0.176
Axis 2:	0.023	0.151	1.362	1.187	0.093

(b) Lanscape-scale Inertia & co-inertia

	Inertia (λ)		Max (λ)		Ratio	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
R/R-L:	4.60	6.453	4.707	6.688	0.978	0.965
Q/Q-L:	2.342	3.745	5.257	8.558	0.446	0.439

	Correlation		Max		Ratio	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
L:	0.176	0.093	0.806	0.714	0.218	0.131

Inertia/Eigenvalues/λ, expresses projected variability; σ, the variance of the set of scores computed for one axis; Cov, the covariance of the two sets of scores projected onto the first and second *RLQ* axes. These values correspond to the latent roots of the analysis; $Cor(x, y)$, the correlation between the two sets of scores for each axis resulting from the *RLQ* analysis; Ratio, the amount of variance preserved between the *RLQ* analysis (Inertia) and the inertia (Max) from the Hill-Smith analysis or correlation from correspondence analyses.

Table D.4: Reproductive trait regional-scale *RLQ* analysis summary statistics showing the comparison of the inertia resulting from (a) the *RLQ* analysis (*RLQ*: three table ordination) which maximises the covariance between traits and the environment mediated by species abundance, and (b) co-inertia analyses ($R - L$ and $Q - L$: two table ordination), the individual parts of the *RLQ* analysis which maximise independently the traits (Hill-Smith analysis of trait variables), the structure of the environment (Hill-Smith analysis of environmental variables) and the correlation (correspondence analysis of sites-species table). The first two axis of the analyses are considered.

(a) Regional-scale RLQ

Total inertia (λ): 0.9594

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
Eigenvalues (λ):	0.841	0.094	0.015	0.006	0.004
Projected inertia (%):	87.57	9.78	1.57	0.56	0.37

	λ decomposition				
	λ	$Cov(Q,R)^2$	σ_R	σ_Q	$Cor(Q,R)$
Axis 1:	0.842	0.917	2.244	1.544	0.265
Axis 2:	0.094	0.307	1.452	1.336	0.158

(b) Regional-scale Inertia & co-inertia

	Inertia (λ)		Max (λ)		Ratio	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
R/R-L:	5.033	7.141	5.141	7.236	0.979	0.987
Q/Q-L:	2.238	4.165	5.257	8.558	0.454	0.487

	Correlation		Max		Ratio	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
L:	0.265	0.158	0.806	0.714	0.329	0.222

Inertia/Eigenvalues/λ, expresses projected variability; σ, the variance of the set of scores computed for one axis; Cov, the covariance of the two sets of scores projected onto the first and second *RLQ* axes. These values correspond to the latent roots of the analysis; $Cor(x, y)$, the correlation between the two sets of scores for each axis resulting from the *RLQ* analysis; Ratio, the amount of variance preserved between the *RLQ* analysis (Inertia) and the inertia (Max) from the Hill-Smith analysis or correlation from correspondence analyses.

(a) Landscape scale **(b)** Regional scale

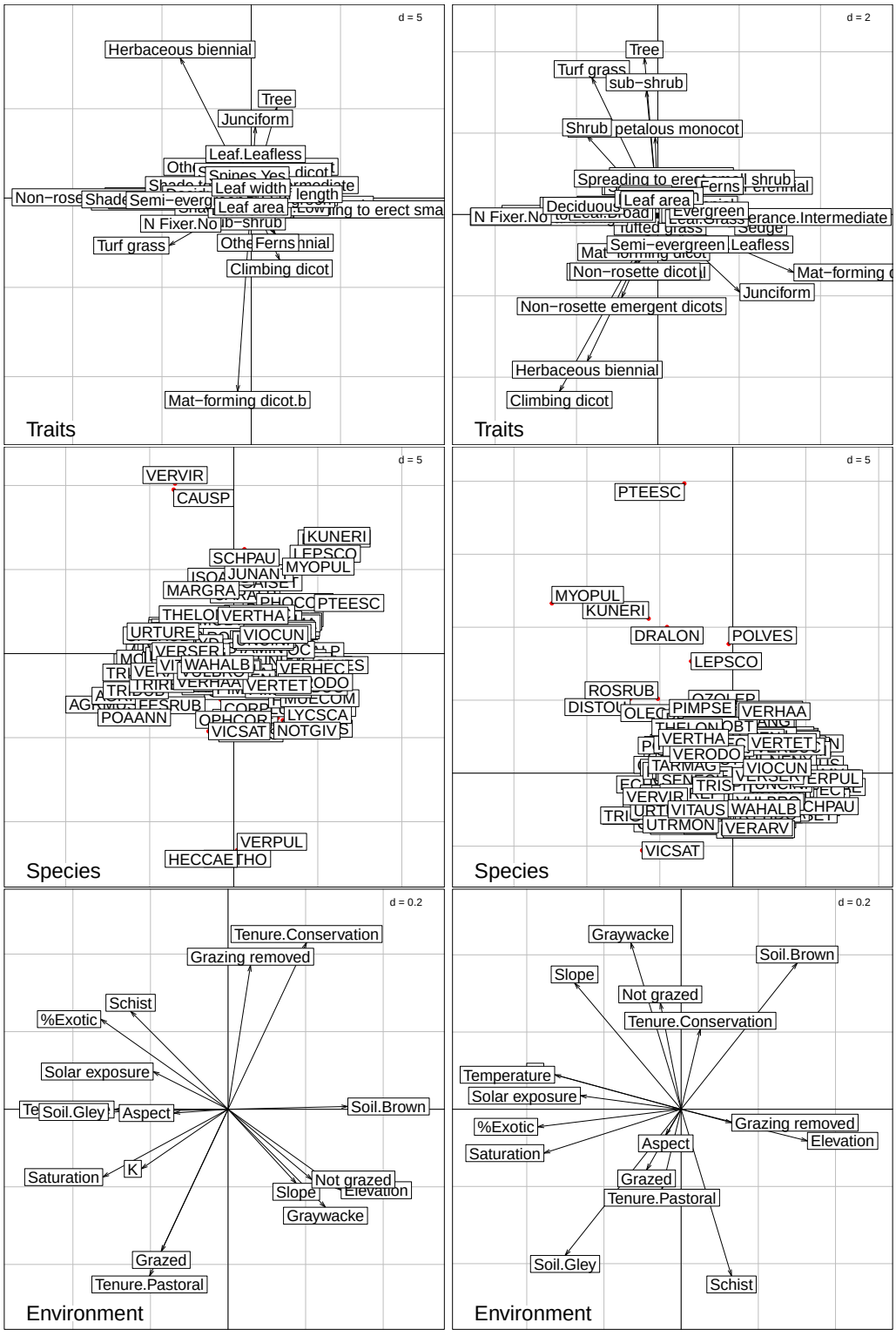


Figure D.1: Vegetative trait (a) landscape-scale and (b) regional-scale *RLQ* biplots showing trait, species and environment ordination scores of the first two axes. Environmental variables associated with land-use show the strongest associations with traits at the landscape scale, whereas phyio-chemical variables show the strongest associations at the regional scale. Species codes are provided in Appendix E.

(a) Landscape scale **(b)** Regional scale

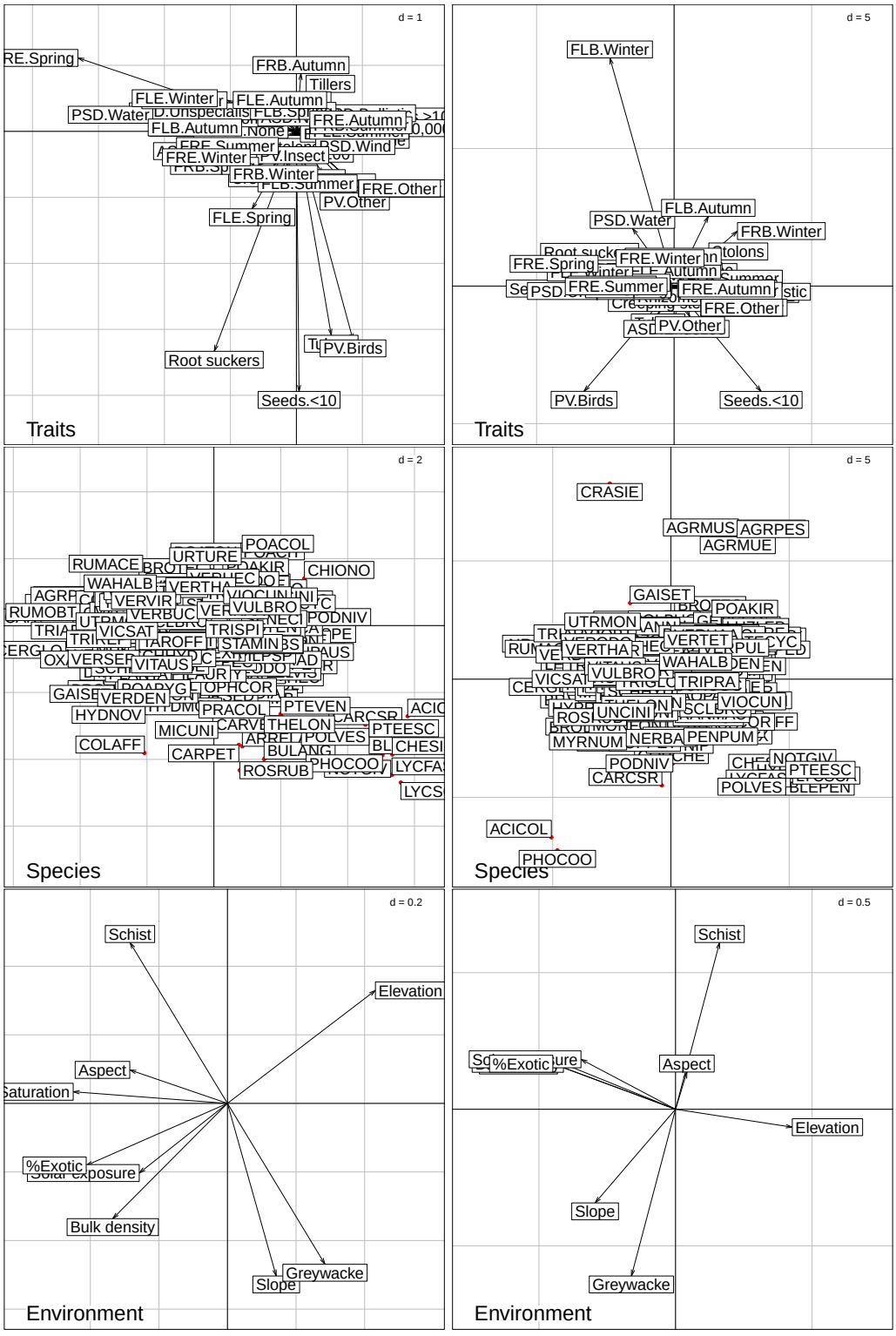
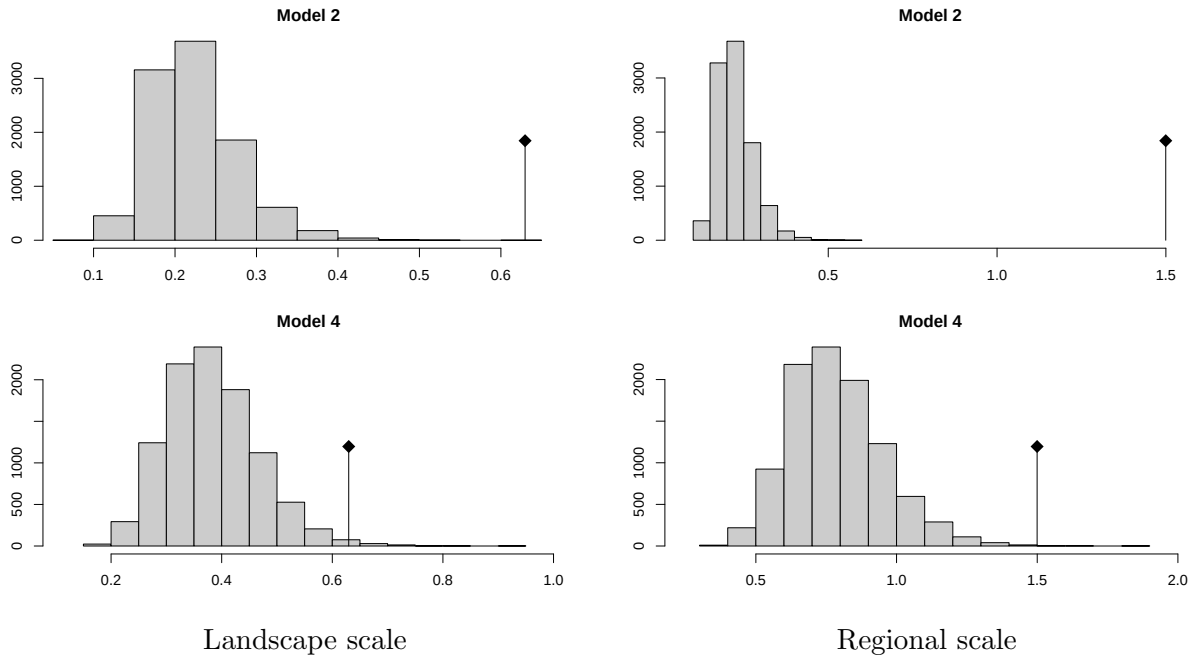
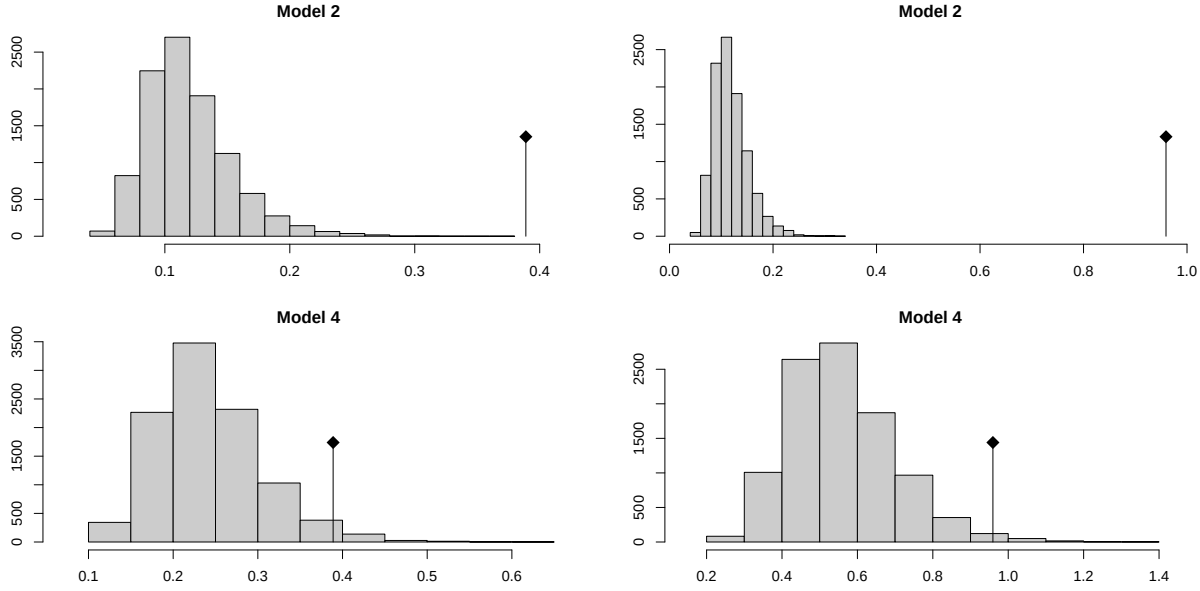


Figure D.2: Reproductive trait (a) landscape-scale and (b) regional-scale *RLQ* biplots showing trait, species and environment ordination scores of the first two axes. Both scales show similar environmental association strengths, whereas clonal reproductive types appear to be more important at the landscape scale and insect pollination more important at the regional scale. Key: GCO = Above ground clonal dispersal organ, BGCO = Below ground clonal dispersal organ, PSD = Passive seed dispersal, ASD = Active seed dispersa, PV = Pollen vector, FLB = Flowering begins, FLE = Flowering ends, FRB = Fruiting begins, FRE = Fruting ends. Species codes are provided in Appendix E.



Landscape scale Regional scale

(a) Vegetative traits



Landscape scale Regional scale

(b) Reproductive traits

Figure D.3: Results of the multivariate procedure used to evaluate the significance of (a) landscape and (b) regional-scale vegetative trait-environment relationships. Bars show permuted expected interia values while the pin shows the observed inertia value. Model 2 tests the link between species and trait composition, while Model 4 tests the link between traits and the environment. Both tests are highly significant at the landscape scale and at the regional scale for both vegetative ($p = 0$ & $p = 0.007$; $p = 0$ & $p = 0.001$) and reproductive traits ($p = 0$ & $p = 0.022$; $p = 0$ & $p = 0.011$) respectively.

Appendix E

Table E.1: Linear Mixed-Effects Models for showing the effect of species abundance and trait uniqueness on change in species abundance between the first (t_1) and second (t_2) sampling periods.

	Model 1	Model 2	Model 3
(Intercept)	-0.182^{***}	-0.807^{***}	0.007
	(0.050)	(0.082)	(0.066)
Abundance t_1		0.004	-0.013^{***}
		(0.003)	(0.003)
Uniqueness t_1		0.004	
		(0.006)	
Abundance t_1 × Uniqueness t_1		-0.000	
		(0.000)	
Uniqueness t_2			-0.002
			(0.005)
Abundance t_1 × Uniqueness t_2			-0.000
			(0.000)
AIC	16041.680	10880.874	6028.760

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.2: Linear Mixed-Effects Models for showing the effect of species abundance and trait uniqueness on change in species abundance between the second (t_2) and third (t_3) sampling periods.

	Model 1	Model 2	Model 3
(Intercept)	0.200^{***}	-0.228^{**}	0.276^{***}
	(0.043)	(0.081)	(0.056)
Abundance t_2		0.002	-0.012^{***}
		(0.004)	(0.003)
Uniqueness t_2		-0.002	
		(0.006)	
Abundance t_2 × Uniqueness t_2		-0.000	
		(0.000)	
Uniqueness t_3			0.005
			(0.004)
Abundance t_2 × Uniqueness t_3			-0.000
			(0.000)
AIC	14262.739	10402.156	5952.414

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.3: Linear Mixed-Effects Models for showing the effect of species abundance and trait uniqueness on change in species abundance between the first (t_1) and third (t_3) sampling periods.

	Model 1	Model 2	Model 3
(Intercept)	0.011	-0.676^{***}	0.260^{***}
	(0.059)	(0.093)	(0.075)
Abundance t_1		0.003	-0.019^{***}
		(0.004)	(0.003)
Uniqueness t_1		0.002	
		(0.007)	
Abundance t_1 $\times$ Uniqueness t_1		-0.000	
		(0.000)	
Uniqueness t_3			-0.003
			(0.006)
Abundance t_1 $\times$ Uniqueness t_3			-0.000
			(0.000)
AIC	17107.171	11486.411	6253.869

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.4: Linear Mixed-Effects Models for showing the effect of species abundance and vegetative and reproductive-trait uniqueness on change in species abundance between the first (t_1) and second (t_2) sampling periods.

	Vegetative traits			Reproductive traits		
	Model 1	Model 2	Model 3	Model 1	Model 2	Model 3
Initial Uniqueness						
(Intercept)	-0.182^{***}	-0.755^{***}	0.025	-0.182^{***}	-0.841^{***}	-0.035
	(0.050)	(0.050)	(0.038)	(0.050)	(0.069)	(0.056)
Abundance t_1		0.004^{**}	-0.015^{***}		$0.005^{\cdot}$	-0.014^{***}
		(0.001)	(0.001)		(0.003)	(0.002)
Uniqueness t_1		-0.002			0.007	
		(0.004)			(0.005)	
Abundance t_1 × Uniqueness t_1		0.000			-0.000	
		(0.000)			(0.000)	
Final Uniqueness						
Uniqueness t_2			-0.008^{*}			0.001
			(0.003)			(0.004)
Abundance t_1 × Uniqueness t_2			0.000			-0.000
			(0.000)			(0.000)
AIC	16041.680	10881.204	6024.569	16041.680	10879.080	6030.034

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.5: Linear Mixed-Effects Models for showing the effect of species abundance and both vegetative and reproductive-trait uniqueness on change in species abundance between the second (t_2) and third (t_3) sampling periods.

	Vegetative traits			Reproductive traits		
	Model 1	Model 2	Model 3	Model 1	Model 2	Model 3
Initial Uniqueness						
(Intercept)	0.200^{***}	-0.184^{***}	0.363^{***}	0.200^{***}	-0.182^{**}	0.297^{***}
	(0.043)	(0.048)	(0.031)	(0.043)	(0.068)	(0.047)
Abundance t_2		-0.001	-0.016^{***}		-0.001	-0.013^{***}
		(0.002)	(0.001)		(0.003)	(0.002)
Uniqueness t_2		-0.010^{*}			-0.006	
		(0.004)			(0.005)	
Abundance t_2 × Uniqueness t_2		$0.000^{\cdot}$			0.000	
		(0.000)			(0.000)	
Final Uniqueness						
Uniqueness t_3			$-0.005^{\cdot}$			0.004
			(0.003)			(0.004)
Abundance t_2 × Uniqueness t_3			0.000			-0.000
			(0.000)			(0.000)
AIC	14262.739	10396.130	5951.459	14262.739	10401.100	5953.069

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.6: Linear Mixed-Effects Models for showing the effect of species abundance and both vegetative and reproductive-trait uniqueness on change in species abundance between the first (t_1) and third (t_3) sampling periods.

	Vegetative traits			Reproductive traits		
	Model 1	Model 2	Model 3	Model 1	Model 2	Model 3
Initial Uniqueness						
(Intercept)	0.011	-0.627^{***}	0.284^{***}	0.011	-0.741^{***}	0.219^{***}
	(0.059)	(0.058)	(0.043)	(0.059)	(0.078)	(0.063)
Abundance t_1		0.002	-0.021^{***}		0.004	-0.019^{***}
		(0.002)	(0.001)		(0.003)	(0.002)
Uniqueness t_1		-0.005			0.008	
		(0.005)			(0.006)	
Abundance t_1 $\times$ Uniqueness t_1		-0.000			-0.000	
		(0.000)			(0.000)	
Final Uniqueness						
Uniqueness t_3			-0.010^{**}			0.001
			(0.004)			(0.005)
Abundance t_1 $\times$ Uniqueness t_3			0.000			-0.000
			(0.000)			(0.000)
AIC	17107.171	11484.477	6247.523	17107.171	11484.472	6254.607

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.7: Linear Mixed-Effects Models for showing the effect of species abundance and trait originality (abundance-weighted vs. presence/absence) on change in species abundance between the first (t_1) and second (t_2) sampling periods.

	Model 1	Model 2	Model 3	Model 4	Model 5
Inercept	-0.182^{***}	-0.635^{***}	0.566^{***}	-0.551^{***}	0.236^{*}
	(0.050)	(0.134)	(0.104)	(0.139)	(0.106)
Abundance t_1		0.000	$-0.006^{\cdot}$	0.001	-0.016^{***}
		(0.005)	(0.004)	(0.005)	(0.004)
Originality t_1		-0.008			
		(0.008)			
Abundance t_1 $\times$ Originality t_1		0.000			
		(0.000)			
Originality t_2			-0.036^{***}		
			(0.006)		
Abundance t_1 $\times$ Originality t_2			-0.001^{**}		
			(0.000)		
Originality$^{p/a}$ t_1				-0.014	
				(0.008)	
Abundance t_1 $\times$ Originality$^{p/a}$ t_1				0.000	
				(0.000)	
Originality$^{p/a}$ t_2					-0.017^{*}
					(0.006)
Abundance t_1 $\times$ Originality$^{p/a}$ t_2					0.000
					(0.000)
AIC	16041.680	10880.259	5956.791	10878.779	6022.966

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.8: Linear Mixed-Effects Models for showing the effect of species abundance and trait originality (abundance-weighted vs. presence/absence) on change in species abundance between the second (t_2) and third (t_3) sampling periods.

	Model 1	Model 2	Model 3	Model 4	Model 5
Inercept	0.200^{***}	0.040	0.721^{***}	-0.048	0.308^{***}
	(0.043)	(0.133)	(0.090)	(0.133)	(0.089)
Abundance t_2		-0.008	-0.008^{*}	-0.003	-0.016^{***}
		(0.006)	(0.004)	(0.006)	(0.004)
Originality t_2		-0.018^{*}			
		(0.008)			
Abundance t_2 × Originality t_2		0.001			
		(0.000)			
Originality t_3			-0.024^{***}		
			(0.005)		
Abundance t_2 × Originality t_3			-0.001^{*}		
			(0.000)		
Originality$^{p/a}$ t_2				-0.013	
				(0.008)	
Abundance t_2 × Originality$^{p/a}$ t_2				0.000	
				(0.000)	
Originality$^{p/a}$ t_3					0.002
					(0.006)
Abundance t_2 × Originality$^{p/a}$ t_3					0.000
					(0.000)
AIC	14262.739	10396.951	5917.383	10400.033	5954.022

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.9: Linear Mixed-Effects Models for showing the effect of species abundance and trait originality (abundance-weighted vs. presence/absence) on change in species abundance between the first (t_1) and third (t_3) sampling periods.

	Model 1	Model 2	Model 3	Model 4	Model 5
Inercept	0.011	-0.382^{*}	1.151^{***}	$-0.281^{\cdot}$	0.497^{***}
	(0.059)	(0.153)	(0.121)	(0.161)	(0.121)
Abundance t_1		-0.006	-0.015^{***}	-0.005	-0.026^{***}
		(0.006)	(0.004)	(0.006)	(0.004)
Originality t_1		$-0.017^{\cdot}$			
		(0.009)			
Abundance t_1 $\times$ Originality t_1		0.001			
		(0.000)			
Originality t_3			-0.058^{***}		
			(0.007)		
Abundance t_1 $\times$ Originality t_3			$-0.000^{\cdot}$		
			(0.000)		
Originality$^{p/a}$ t_2				-0.025^{*}	
				(0.010)	
Abundance t_1 $\times$ Originality$^{p/a}$ t_2				0.000	
				(0.000)	
Originality$^{p/a}$ t_3					-0.018^{*}
					(0.008)
Abundance t_1 $\times$ Originality$^{p/a}$ t_3					0.000
					(0.000)
AIC	17107.171	11482.479	6162.681	11480.368	6248.959

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.10: Linear Mixed-Effects Models for showing the effect of species abundance and both vegetative and reproductive-trait originality on change in species abundance between the first (t_1) and second (t_2) sampling periods.

	Vegetative traits			Reproductive traits		
	Model 1	Model 2	Model 3	Model 1	Model 2	Model 3
Inercept	-0.182^{***}	-0.617^{***}	0.398^{***}	-0.182^{***}	-0.757^{***}	0.549^{***}
	(0.050)	(0.122)	(0.100)	(0.050)	(0.133)	(0.102)
Abundance t_1		0.003	-0.004		-0.000	-0.008^{*}
		(0.005)	(0.004)		(0.005)	(0.003)
Originality t_1		-0.009			-0.001	
		(0.007)			(0.008)	
Abundance t_1 $\times$ Originality t_1		0.000			0.000	
		(0.000)			(0.000)	
Originality t_2			-0.025^{***}			-0.034^{***}
			(0.006)			(0.006)
Abundance t_1 $\times$ Originality t_2			-0.001^{**}			-0.001^{*}
			(0.000)			(0.000)
AIC	16041.680	10879.371	5965.852	16041.680	10880.391	5967.406

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.11: Linear Mixed-Effects Models for showing the effect of species abundance and both vegetative and reproductive-trait originality on change in species abundance between the second (t_2) and third (t_3) sampling periods.

	Vegetative traits			Reproductive traits		
	Model 1	Model 2	Model 3	Model 1	Model 2	Model 3
Inercept	0.200^{***}	-0.091	0.688^{***}	0.200^{***}	-0.084	0.630^{***}
	(0.043)	(0.127)	(0.087)	(0.043)	(0.129)	(0.088)
Abundance t_2		-0.005	-0.008^{*}		-0.005	-0.008^{*}
		(0.006)	(0.004)		(0.005)	(0.004)
Originality t_2		-0.010			-0.010	
		(0.007)			(0.007)	
Abundance t_2 $\times$ Originality t_2		0.000			0.000	
		(0.000)			(0.000)	
Originality t_3			-0.022^{***}			-0.018^{***}
			(0.005)			(0.005)
Abundance t_2 $\times$ Originality t_3			-0.001^{*}			-0.001^{*}
			(0.000)			(0.000)
AIC	14262.739	10400.565	5914.315	14262.739	10400.392	5927.547

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.12: Linear Mixed-Effects Models for showing the effect of species abundance and both vegetative and reproductive-trait originality on change in species abundance between the first (t_1) and third (t_3) sampling periods.

	Vegetative traits			Reproductive traits		
	Model 1	Model 2	Model 3	Model 1	Model 2	Model 3
Inercept	0.011	-0.380^{**}	0.899^{***}	0.011	-0.641^{***}	1.105^{***}
	(0.059)	(0.139)	(0.114)	(0.059)	(0.153)	(0.121)
Abundance t_1		-0.004	-0.011^{**}		-0.004	-0.016^{***}
		(0.006)	(0.004)		(0.005)	(0.004)
Originality t_1		-0.017^{*}			-0.001	
		(0.008)			(0.009)	
Abundance t_1 $\times$ Originality t_1		0.000			0.000	
		(0.000)			(0.000)	
Originality t_3			-0.042^{***}			-0.055^{***}
			(0.007)			(0.007)
Abundance t_1 $\times$ Originality t_3			-0.001^{*}			-0.000
			(0.000)			(0.000)
AIC	17107.171	11481.956	6170.802	17107.171	11484.822	6181.653

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.13: Linear Mixed-Effects Models showing the effect of species abundance and difference in community-trait optimum (Δ *CTO*) on change in species abundance between the first (t_1) and second (t_2) sampling periods.

	Model 1	Model 2	Model 3
Intercept	-0.130^{*}	-0.137^{*}	-0.738^{***}
	(0.055)	(0.055)	(0.049)
ΔCTO		0.007^{***}	-0.004^{**}
		(0.001)	(0.001)
Abundance t_1			0.003^{***}
			(0.000)
Abundance t_1 $\times$ ΔCTO			0.000^{***}
			(0.000)
AIC	1306260.753	1306237.569	857310.858

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.14: Linear Mixed-Effects Models showing the effect of species abundance and difference in community-trait optimum (Δ *CTO*) on change in species abundance between the second (t_2) and third (t_3) sampling periods.

	Model 1	Model 2	Model 3
Intercept	0.178^{***}	0.176^{***}	-0.266^{***}
	(0.052)	(0.052)	(0.052)
ΔCTO		0.003^{*}	-0.005^{**}
		(0.001)	(0.001)
Abundance t_2			-0.000^{**}
			(0.000)
Abundance t_2 $\times$ ΔCTO			0.000^{**}
			(0.000)
AIC	1153966.018	1153963.414	818974.821

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.15: Linear Mixed-Effects Models showing the effect of species abundance and difference in community-trait optimum ($\Delta\ CTO$) on change in species abundance between the first (t_1) and third (t_3) sampling periods.

	Model 1	Model 2	Model 3
Intercept	0.027	0.020	-0.634^{***}
	(0.063)	(0.063)	(0.058)
ΔCTO		0.007^{***}	-0.004^{*}
		(0.001)	(0.002)
Abundance t_1			0.001^{***}
			(0.000)
Abundance t_1 $\times$ ΔCTO			0.000^{**}
			(0.000)
AIC	1390882.978	1390856.726	907154.395

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.16: Linear Mixed-Effects Models showing the effect of species abundance and difference in community-trait optimum ($\Delta\ CTO$), for both vegetative and reproductive-traits, on change in species abundance between the first (t_1) and second (t_2) sampling periods.

	Vegetative traits			Reproductive traits		
	Model 1	Model 2	Model 3	Model 1	Model 2	Model 3
Intercept	-0.131^{*}	-0.137^{*}	-0.739^{***}	-0.131^{*}	-0.139^{*}	-0.738^{***}
	(0.055)	(0.055)	(0.049)	(0.055)	(0.055)	(0.049)
$\Delta\ CTO$		0.006^{**}	-0.004^{*}		0.008^{***}	-0.004^{*}
		(0.002)	(0.002)		(0.002)	(0.002)
Abundance t_1			0.003^{***}			0.003^{***}
			(0.000)			(0.000)
Abundance $t_1 \times \Delta\ CTO$			0.000^{**}			0.001^{***}
			(0.000)			(0.000)
AIC	608698.914	608690.836	399937.185	699701.347	699687.390	459607.520

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.17: Linear Mixed-Effects Models showing the effect of species abundance and difference in community-trait optimum ($\Delta\ CTO$), for both vegetative and reproductive-traits, on change in species abundance between the second (t_2) and third (t_3) sampling periods.

	Vegetative traits			Reproductive traits		
	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
Intercept	0.178^{***}	0.174^{***}	-0.251^{***}	0.178^{***}	0.171^{**}	-0.248^{***}
	(0.052)	(0.052)	(0.051)	(0.052)	(0.052)	(0.051)
$\Delta\ CTO$		0.004^{*}	-0.003		0.007^{***}	-0.006^{**}
		(0.002)	(0.002)		(0.002)	(0.002)
Abundance t_2			-0.000			-0.001^{*}
			(0.000)			(0.000)
Abundance $t_2 \times \Delta\ CTO$			0.000			0.000^{*}
			(0.000)			(0.000)
AIC	553035.678	553031.109	392741.820	647115.381	647105.260	459434.854

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.18: Linear Mixed-Effects Models showing the effect of species abundance and difference in community-trait optimum ($\Delta\ CTO$), for both vegetative and reproductive-traits, on change in species abundance between the first (t_1) and third (t_3) sampling periods.

	Vegetative traits			Reproductive traits		
	Model 1	Model 2	Model 3	Model 1	Model 2	Model 3
Intercept	0.027	0.021	-0.634^{***}	0.027	0.020	-0.634^{***}
	(0.063)	(0.063)	(0.057)	(0.063)	(0.063)	(0.058)
$\Delta\ CTO$		0.007^{***}	$-0.004^{\cdot}$		0.007^{***}	-0.003
		(0.002)	(0.002)		(0.002)	(0.002)
Abundance t_1			0.001^{***}			0.001^{***}
			(0.000)			(0.000)
Abundance $t_1 \times \Delta\ CTO$			0.000^{*}			0.000^{*}
			(0.000)			(0.000)
AIC	648073.522	648063.268	423105.014	744977.181	744962.460	486258.093

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

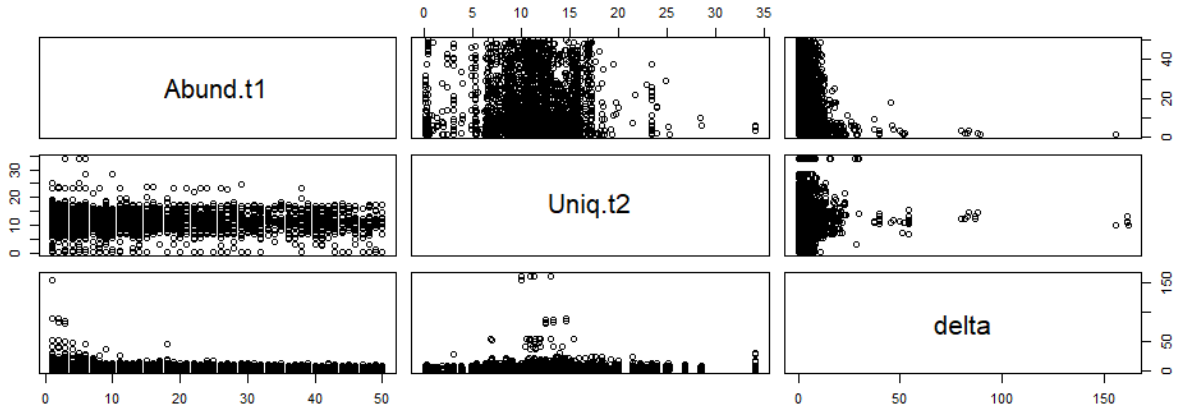


Figure E.1: Plots showing the values of initial abundance (*abund.t*1), final trait uniqueness (*uniq.t*2) and distance from the community selected trait optimum (*delta*) plotted against each other for the full trait dataset of the first (1980's) to final (2000's) study period.

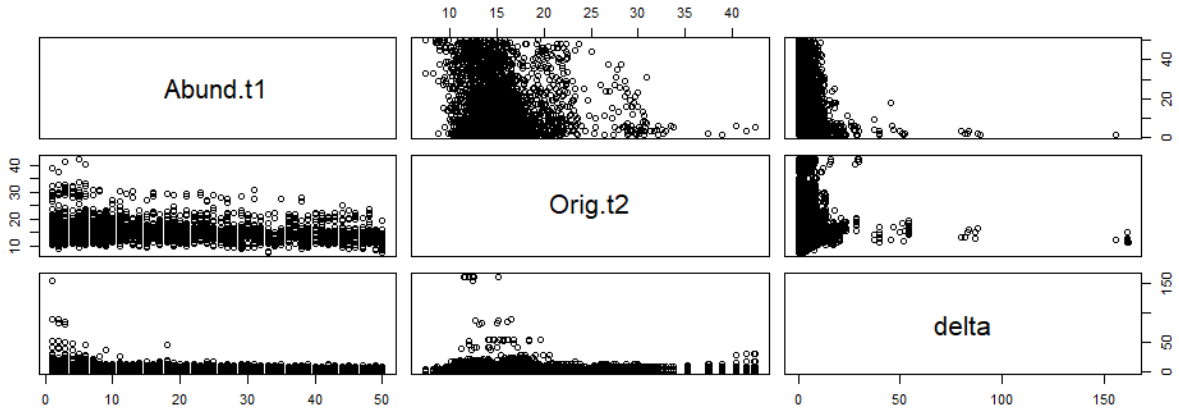


Figure E.2: Plots showing the values of initial abundance (*abund.t*1), final trait originality (*orig.t*2) and distance from the community selected trait optimum (*delta*) plotted against each other for the full trait dataset of the first (1980's) to final (2000's) study period.

Table E.19: Linear Mixed-Effects Models showing the effect of species abundance, vegetative-trait uniqueness and Δtrait optimum on change in species abundance between the first (t_1) and second (t_2) sampling periods.

	Uniqueness t_1	Uniqueness t_2
Intercept	-0.707^{***}	0.018
	(0.049)	(0.037)
Abundance t_1	0.003^{***}	-0.015^{***}
	(0.000)	(0.000)
Uniqueness t_1	-0.005^{***}	
	(0.001)	
Δ *CTO*	-0.004	0.002
	(0.003)	(0.002)
Abundance t_1 × Uniqueness t_1	0.000	
	(0.000)	
Abundance t_1 × Δ *CTO*	0.000^{**}	-0.000
	(0.000)	(0.000)
Uniqueness t_1 × Δ *CTO*	-0.000	
	(0.000)	
Uniqueness t_2		-0.007^{***}
		(0.001)
Abundance t_1 × Uniqueness t_2		0.000^{***}
		(0.000)
Uniqueness t_2 × Δ *CTO*		-0.000
		(0.000)
AIC	399861.273	210046.798

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.20: Linear Mixed-Effects Models showing the effect of species abundance, vegetative-trait uniqueness and Δtrait optimum on change in species abundance between the second (t_2) and third (t_3) sampling periods.

	Uniqueness t_2	Uniqueness t_3
Intercept	-0.175^{***}	0.330^{***}
	(0.051)	(0.036)
Abundance t_2	-0.002^{***}	-0.016^{***}
	(0.000)	(0.000)
Uniqueness t_2	-0.012^{***}	
	(0.001)	
Δ *CTO*	-0.003	$0.004^{\cdot}$
	(0.003)	(0.002)
Abundance t_2 × Uniqueness t_2	0.000^{***}	
	(0.000)	
Abundance t_2 × Δ *CTO*	0.000	-0.000^{**}
	(0.000)	(0.000)
Uniqueness t_2 × Δ *CTO*	0.000	
	(0.000)	
Uniqueness t_3		-0.005^{***}
		(0.001)
Abundance t_2 × Uniqueness t_3		0.000^{***}
		(0.000)
Uniqueness t_3 × Δ *CTO*		-0.000
		(0.000)
AIC	392448.840	212591.504

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.21: Linear Mixed-Effects Models showing the effect of species abundance, vegetative-trait uniqueness and Δtrait optimum on change in species abundance between the first (t_1) and third (t_3) sampling periods.

	Uniqueness t_1	Uniqueness t_3
Intercept	-1.489^{***}	-0.166^{*}
	(0.059)	(0.077)
Abundance t_1	0.013^{***}	-0.005^{***}
	(0.001)	(0.001)
Uniqueness t_1	0.010^{***}	
	(0.001)	
Δ *CTO*	-0.006	0.002
	(0.004)	(0.004)
Abundance t_1 × Uniqueness t_1	-0.000^{**}	
	(0.000)	
Abundance t_1 × Δ *CTO*	$0.001^{\cdot}$	-0.000
	(0.000)	(0.000)
Uniqueness t_1 × Δ *CTO*	0.000	
	(0.000)	
Uniqueness t_3		-0.027^{***}
		(0.002)
Abundance t_1 × Uniqueness t_3		-0.000
		(0.000)
Uniqueness t_3 × Δ *CTO*		-0.000
		(0.000)
AIC	75400.798	6692.234

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.22: Linear Mixed-Effects Models showing the effect of species abundance, reproductive-trait uniqueness and Δtrait optimum on change in species abundance between the first (t_1) and second (t_2) sampling periods.

	Uniqueness t_1	Uniqueness t_2
Intercept	-0.751^{***}	-0.043
	(0.050)	(0.038)
Abundance t_1	0.002^{***}	-0.014^{***}
	(0.000)	(0.000)
Uniqueness t_1	0.001	
	(0.001)	
Δ *CTO*	$-0.008^{\cdot}$	-0.003
	(0.004)	(0.003)
Abundance t_1 × Uniqueness t_1	0.000	
	(0.000)	
Abundance t_1 × Δ *CTO*	0.001^{***}	-0.000
	(0.000)	(0.000)
Uniqueness t_1 × Δ *CTO*	0.000	
	(0.000)	
Uniqueness t_2		0.001^{*}
		(0.001)
Abundance t_1 × Uniqueness t_2		-0.000
		(0.000)
Uniqueness t_2 × Δ *CTO*		0.000
		(0.000)
AIC	459605.232	241452.275

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.23: Linear Mixed-Effects Models showing the effect of species abundance, reproductive-trait uniqueness and Δtrait optimum on change in species abundance between the second (t_2) and third (t_3) sampling periods.

	Uniqueness t_2	Uniqueness t_3
Intercept	-0.499^{***}	0.236^{***}
	(0.067)	(0.042)
Abundance t_2	0.003^{***}	-0.014^{***}
	(0.001)	(0.001)
Uniqueness t_2	-0.007^{***}	
	(0.001)	
Δ *CTO*	-0.018^{**}	0.000
	(0.006)	(0.004)
Abundance t_2 × Uniqueness t_2	0.000^{***}	
	(0.000)	
Abundance t_2 × Δ *CTO*	-0.000	-0.001^{**}
	(0.000)	(0.000)
Uniqueness t_2 × Δ *CTO*	0.001^{**}	
	(0.000)	
Uniqueness t_3		0.000
		(0.001)
Abundance t_2 × Uniqueness t_3		-0.000
		(0.000)
Uniqueness t_3 × Δ *CTO*		0.000
		(0.000)
AIC	241682.693	90544.909

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.24: Linear Mixed-Effects Models showing the effect of species abundance, reproductive-trait uniqueness and Δtrait optimum on change in species abundance between the first (t_1) and third (t_3) sampling periods.

	Uniqueness t_1	Uniqueness t_3
Intercept	-1.388^{***}	-0.224^{**}
	(0.060)	(0.079)
Abundance t_1	0.012^{***}	0.004^{***}
	(0.001)	(0.001)
Uniqueness t_1	-0.004^{**}	
	(0.001)	
Δ *CTO*	0.002	-0.002
	(0.006)	(0.006)
Abundance t_1 × Uniqueness t_1	-0.000	
	(0.000)	
Abundance t_1 × Δ *CTO*	$0.001^{\cdot}$	0.000
	(0.000)	(0.000)
Uniqueness t_1 × Δ *CTO*	-0.000	
	(0.001)	
Uniqueness t_3		-0.008^{***}
		(0.002)
Abundance t_1 × Uniqueness t_3		-0.001^{***}
		(0.000)
Uniqueness t_3 × Δ *CTO*		0.000
		(0.000)
AIC	86570.476	7604.987

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.25: Linear Mixed-Effects Models showing the effect of species abundance, vegetative-trait Originality and Δtrait optimum on change in species abundance between the first (t_1) and second (t_2) sampling periods.

	Originality t_1	Originality t_2
Intercept	-0.604^{***}	0.654^{***}
	(0.053)	(0.043)
Abundance t_1	0.004^{***}	-0.004^{***}
	(0.001)	(0.001)
Originality t_1	-0.008^{***}	
	(0.001)	
Δ *CTO*	0.002	0.005
	(0.006)	(0.005)
Abundance t_1 × Originality t_1	-0.000^{*}	
	(0.000)	
Abundance t_1 × Δ *CTO*	0.000^{**}	0.000
	(0.000)	(0.000)
Originality t_1 × Δ *CTO*	-0.000	
	(0.000)	
Originality t_2		-0.041^{***}
		(0.001)
Abundance t_1 × Originality t_2		-0.001^{***}
		(0.000)
Originality t_2 × Δ *CTO*		-0.000
		(0.000)
AIC	399865.233	206569.658

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.26: Linear Mixed-Effects Models showing the effect of species abundance, vegetative-trait Originality and Δtrait optimum on change in species abundance between the second (t_2) and third (t_3) sampling periods.

	Originality t_2	Originality t_3
Intercept	0.031	0.951^{***}
	(0.057)	(0.041)
Abundance t_2	-0.007^{***}	-0.012^{***}
	(0.001)	(0.001)
Originality t_2	-0.017^{***}	
	(0.001)	
Δ CTO	$-0.010^{\cdot}$	-0.000
	(0.006)	(0.004)
Abundance t_2 × Originality t_2	0.000^{***}	
	(0.000)	
Abundance t_2 × Δ CTO	0.000	$-0.000^{\cdot}$
	(0.000)	(0.000)
Originality t_2 × Δ CTO	0.001	
	(0.000)	
Originality t_3		-0.040^{***}
		(0.001)
Abundance t_2 × Originality t_3		-0.000^{***}
		(0.000)
Originality t_3 × Δ CTO		0.000
		(0.000)
AIC	392595.858	210272.909

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.27: Linear Mixed-Effects Models showing the effect of species abundance, vegetative-trait Originality and Δtrait optimum on change in species abundance between the first (t_1) and third (t_3) sampling periods.

	Originality t_1	Originality t_3
Intercept	-1.517^{***}	0.184^{*}
	(0.067)	(0.092)
Abundance t_1	0.017^{***}	0.017^{***}
	(0.002)	(0.002)
Originality t_1	0.005^{**}	
	(0.002)	
Δ *CTO*	0.000	-0.003
	(0.008)	(0.008)
Abundance t_1 × Originality t_1	-0.000^{**}	
	(0.000)	
Abundance t_1 × Δ *CTO*	$0.001^{\cdot}$	-0.000
	(0.000)	(0.000)
Originality t_1 × Δ *CTO*	-0.000	
	(0.000)	
Originality t_3		-0.030^{***}
		(0.003)
Abundance t_1 × Originality t_3		-0.002^{***}
		(0.000)
Originality t_3 × Δ *CTO*		0.000
		(0.000)
AIC	75497.214	6479.190

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.28: Linear Mixed-Effects Models showing the effect of species abundance, reproductive-trait Originality and Δtrait optimum on change in species abundance between the first (t_1) and second (t_2) sampling periods.

	Originality t_1	Originality t_2
Intercept	-0.593^{***}	1.304^{***}
	(0.055)	(0.046)
Abundance t_1	-0.002^{**}	-0.011^{***}
	(0.001)	(0.000)
Originality t_1	-0.009^{***}	
	(0.002)	
Δ *CTO*	-0.004	0.011^{**}
	(0.005)	(0.004)
Abundance t_1 × Originality t_1	0.000^{***}	
	(0.000)	
Abundance t_1 × Δ *CTO*	0.000^{**}	0.000
	(0.000)	(0.000)
Originality t_1 × Δ *CTO*	0.000	
	(0.000)	
Originality t_2		-0.081^{***}
		(0.001)
Abundance t_1 × Originality t_2		-0.000^{***}
		(0.000)
Originality t_2 × Δ *CTO*		$-0.000^{\cdot}$
		(0.000)
AIC	459552.788	235509.685

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.29: Linear Mixed-Effects Models showing the effect of species abundance, reproductive-trait Originality and Δtrait optimum on change in species abundance between the second (t_2) and third (t_3) sampling periods.

	Originality t_2	Originality t_3
Intercept	0.057	1.074^{***}
	(0.079)	(0.052)
Abundance t_2	-0.002	-0.008^{***}
	(0.001)	(0.001)
Originality t_2	-0.039^{***}	
	(0.003)	
Δ CTO	-0.001	0.006
	(0.007)	(0.004)
Abundance t_2 × Originality t_2	0.001^{***}	
	(0.000)	
Abundance t_2 × Δ CTO	-0.000	-0.000^{*}
	(0.000)	(0.000)
Originality t_2 × Δ CTO	0.000	
	(0.000)	
Originality t_3		-0.052^{***}
		(0.002)
Abundance t_2 × Originality t_3		-0.001^{***}
		(0.000)
Originality t_3 × Δ CTO		-0.000
		(0.000)
AIC	241488.651	89368.985

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$

Table E.30: Linear Mixed-Effects Models showing the effect of species abundance, reproductive-trait Originality and Δtrait optimum on change in species abundance between the first (t_1) and third (t_3) sampling periods.

	Originality t_1	Originality t_3
Intercept	-0.849^{***}	0.193^{*}
	(0.072)	(0.098)
Abundance t_1	-0.004^{*}	0.020^{***}
	(0.002)	(0.002)
Originality t_1	-0.036^{***}	
	(0.003)	
Δ CTO	0.000	0.000
	(0.007)	(0.006)
Abundance t_1 $\times$ Originality t_1	0.001^{***}	
	(0.000)	
Abundance t_1 $\times$ Δ CTO	0.000	0.000
	(0.000)	(0.000)
Originality t_1 $\times$ Δ CTO	-0.000	
	(0.000)	
Originality t_3		-0.029^{***}
		(0.004)
Abundance t_1 $\times$ Originality t_3		-0.002^{***}
		(0.000)
Originality t_3 $\times$ Δ CTO		0.000
		(0.000)
AIC	86367.363	7321.991

$^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{\cdot}p < 0.1$